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Preface

Concepts of Biology is intended for the introductory biology course for non-science majors taught at most two- and four-year colleges. The scope, sequence, and level of the program are designed to match typical course syllabi. This text includes interesting features that make connections between scientific concepts and the everyday world of students. *Concepts of Biology* conveys the major themes of biology, such as a foundation in evolution, and features a rich and engaging art program.

Welcome to *Concepts of Biology*, an OpenStax resource. This textbook has been created with several goals in mind: accessibility, customization, and student engagement—all while encouraging students toward high levels of academic scholarship. Instructors and students alike will find that this textbook offers a strong introduction to biology in an accessible format.

About OpenStax

OpenStax is a non-profit organization committed to improving student access to quality learning materials. Our free textbooks are developed and peer-reviewed by educators to ensure they are readable, accurate, and meet the scope and sequence requirements of today's college courses. Unlike traditional textbooks, OpenStax resources live online and are owned by the community of educators using them. Through our partnerships with companies and foundations committed to reducing costs for students, OpenStax is working to improve access to higher education for all. OpenStax is an initiative of Rice University and is made possible through the generous support of several philanthropic foundations.

About OpenStax's Resources

OpenStax resources provide quality academic instruction. Three key features set our materials apart from others: they can be customized by instructors for each class, they are a “living” resource that grows online through contributions from science educators, and they are available free or for minimal cost.

Customization

OpenStax learning resources are designed to be customized for each course. Our textbooks provide a solid foundation on which instructors can build, and our resources are conceived and written with flexibility in mind. Instructors can select the sections most relevant to their curricula and create a textbook that speaks directly to the needs of their classes and student body. Teachers are encouraged to expand on existing examples by adding unique context via geographically localized applications and topical connections.

Instructors also have the option of creating a customized version of their OpenStax book. The custom version can be made available to students in low-cost print or digital form through their campus bookstore. Visit your book page on openstax.org for more information.

Curation

To broaden access and encourage community curation, *Concepts of Biology* is “open source” licensed under a Creative Commons Attribution (CC-BY) license. The scientific community is invited to submit examples, emerging research, and other feedback to enhance and strengthen the material and keep it current and relevant for today’s students. You can submit your suggestions to Support@OpenStax.org.

Cost

Our textbooks are available for free online, and in low-cost print and e-book editions.

About *Concepts of Biology*

Concepts of Biology is designed for the single-semester introduction to biology course for non-science majors, which for many students is their

only college-level science course. As such, this course represents an important opportunity for students to develop the necessary knowledge, tools, and skills to make informed decisions as they continue with their lives. Rather than being mired down with facts and vocabulary, the typical non-science major student needs information presented in a way that is easy to read and understand. Even more importantly, the content should be meaningful. Students do much better when they understand why biology is relevant to their everyday lives. For these reasons, *Concepts of Biology* is grounded on an evolutionary basis and includes exciting features that highlight careers in the biological sciences and everyday applications of the concepts at hand. We also strive to show the interconnectedness of topics within this extremely broad discipline. In order to meet the needs of today's instructors and students, we maintain the overall organization and coverage found in most syllabi for this course. A strength of *Concepts of Biology* is that instructors can customize the book, adapting it to the approach that works best in their classroom. *Concepts of Biology* also includes an innovative art program that incorporates critical thinking and clicker questions to help students understand—and apply—key concepts.

Coverage and Scope

Our *Concepts of Biology* textbook adheres to the scope and sequence of most one-semester non-majors courses nationwide. We also strive to make biology, as a discipline, interesting and accessible to students. In addition to a comprehensive coverage of core concepts and foundational research, we have incorporated features that draw learners into the discipline in meaningful ways. Our scope of content was developed after surveying over a hundred biology professors and listening to their coverage needs. We provide a thorough treatment of biology's fundamental concepts with a scope that is manageable for instructors and students alike.

Unit 1: The Cellular Foundation of Life. Our opening unit introduces students to the sciences, including the process of science and the underlying concepts from the physical sciences that provide a framework within which learners comprehend biological processes.

Additionally, students will gain solid understanding of the structures, functions, and processes of the most basic unit of life: the cell.

Unit 2: Cell Division and Genetics. Our genetics unit takes learners from the foundations of cellular reproduction to the experiments that revealed the basis of genetics and laws of inheritance.

Unit 3: Molecular Biology and Biotechnology. Students will learn the intricacies of DNA, protein synthesis, and gene regulation and current applications of biotechnology and genomics.

Unit 4: Evolution and the Diversity of Life. The core concepts of evolution are discussed in this unit with examples illustrating evolutionary processes. Additionally, the evolutionary basis of biology reappears throughout the textbook in general discussion and is reinforced through special call-out features highlighting specific evolution-based topics. The diversity of life is explored with detailed study of various organisms and discussion of emerging phylogenetic relationships between and among bacteria, protist kingdoms, fungi, plants, and animals.

Unit 5: Animal Structure and Function. An introduction to the form and function of the animal body is followed by chapters on the immune system and animal development. This unit touches on the biology of all organisms while maintaining an engaging focus on human anatomy and physiology that helps students connect to the topics.

Unit 6: Ecology. Ecological concepts are broadly covered in this unit, with features highlighting localized, real-world issues of conservation and biodiversity.

Pedagogical Foundation and Features

Because of the impact science has on students and society, an important goal of science education is to achieve a scientifically literate population that consistently makes informed decisions. Scientific literacy transcends a basic understanding of scientific principles and processes to include the ability to make sense of the myriad instances where people encounter science in day-to-day life. Thus, a scientifically literate person is one who uses science content knowledge to make informed decisions, either

personally or socially, about topics or issues that have a connection with science. Concepts of Biology is grounded on a solid scientific base and designed to promote scientific literacy. Throughout the text, you will find features that engage the students in scientific inquiry by taking selected topics a step further.

Evolution in Action features uphold the importance of evolution to all biological study through discussions like “Global Decline of Coral Reefs” and “The Red Queen Hypothesis.”

Career in Action features present information on a variety of careers in the biological sciences, introducing students to the educational requirements and day-to-day work life of a variety of professions, such as forensic scientists, registered dietitians, and biogeographers.

Biology in Action features tie biological concepts to emerging issues and discuss science in terms of everyday life. Topics include “Invasive Species” and “Photosynthesis at the Grocery Store.”

Art and Animations that Engage

Our art program takes a straightforward approach designed to help students learn the concepts of biology through simple, effective illustrations, photos, and micrographs. Concepts of Biology also incorporates links to relevant animations and interactive exercises that help bring biology to life for students.

Art Connection features call out core figures in each chapter for student attention. Questions about key figures, including clicker questions that can be used in the classroom, engage students’ critical thinking and analytical abilities to ensure their genuine understanding of the concept at hand.

Concepts in Action features direct students to online interactive exercises and animations to add a fuller context and examples to core content.

About Our Team

Concepts of Biology would not be possible if not for the tremendous contributions of the authors and community reviewing team

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Learning Resources

Wiley Plus for Biology-Fall 2013 Pilot

WileyPLUS provides an engaging online environment for effective teaching and learning. WileyPLUS builds students' confidence because it takes the guesswork out of studying by providing a clear roadmap; what to do, how to do it, and if they did it right. With WileyPLUS, students take more initiative. Therefore, the course has a greater impact on their learning experience. Adaptive tools provide students with a personal, adaptive learning experience so they can build their proficiency on topics and use their study time most effectively. Please let us know if you would like to participate in a Fall 2013 Pilot.

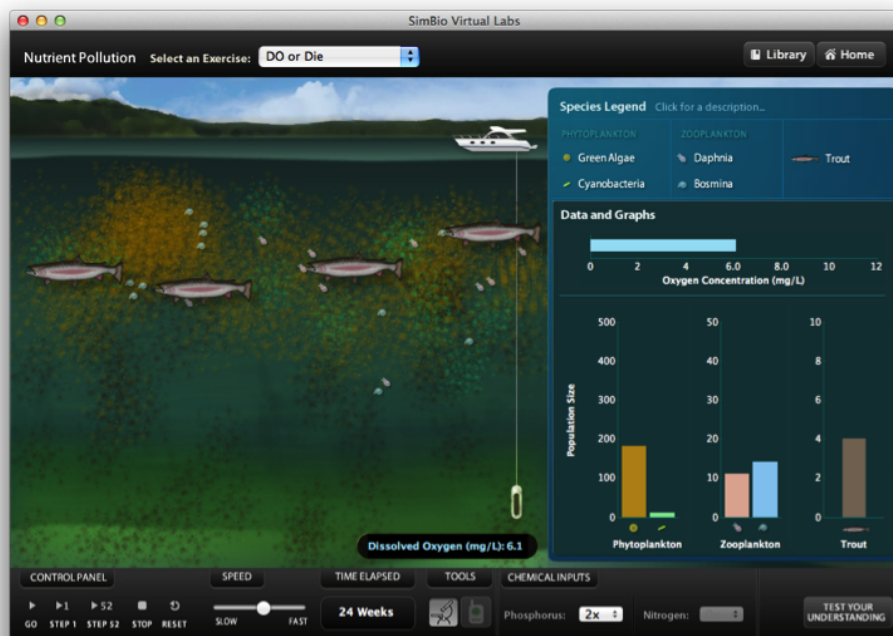
Concepts of Biology Powerpoint Slides (faculty only)

The PowerPoint slides are based on the extensive illustrations from College Physics. They can be edited, incorporated into lecture notes, and you are free to share with anyone in the community. This is a restricted item requiring faculty registration. NOTE: This file is very large and may take some time to download.

SimBio (Laboratory)

SimBio's interactive modules (virtual labs and interactive tutorials and chapters) provide engaging, discovery-based learning tools that complement many of the chapters of Concepts of Biology. SimBio is best known for their EcoBeaker® and EvoBeaker® suites of simulated ecology and evolution laboratories that guide students through the "discovery" of important concepts via a mix of structured and open-ended experimentation on simulated systems. In response to popular demand, SimBio has begun applying the same powerful approaches to topics in cell biology, genetics,

and neurobiology. All of SimBio's modules include instant-feedback questions that enhance student comprehension and auto-graded questions that facilitate implementation.



Introduction

class="introduction"

This NASA image is a composite of several satellite-based views of Earth. To make the whole-Earth image, NASA scientists combine observations of different parts of the planet.

(credit: modification of work by NASA)



Viewed from space, Earth ([\[link\]](#)) offers few clues about the diversity of life forms that reside there. The first forms of life on Earth are thought to have been microorganisms that existed for billions of years before plants and animals appeared. The mammals, birds, and flowers so familiar to us are all relatively recent, originating 130 to 200 million years ago. Humans have inhabited this planet for only the last 2.5 million years, and only in the last 200,000 years have humans started looking like we do today.

Themes and Concepts of Biology

By the end of this section, you will be able to:

- Identify and describe the properties of life
- Describe the levels of organization among living things
- List examples of different sub disciplines in biology

Biology is the science that studies life. What exactly is life? This may sound like a silly question with an obvious answer, but it is not easy to define life. For example, a branch of biology called virology studies viruses, which exhibit some of the characteristics of living entities but lack others. It turns out that although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life.

From its earliest beginnings, biology has wrestled with four questions: What are the shared properties that make something “alive”? How do those various living things function? When faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them? And, finally—what biologists ultimately seek to understand—how did this diversity arise and how is it continuing? As new organisms are discovered every day, biologists continue to seek answers to these and other questions.

Properties of Life

All groups of living organisms share several key characteristics or functions: order, sensitivity or response to stimuli, reproduction, adaptation, growth and development, regulation, homeostasis, and energy processing. When viewed together, these eight characteristics serve to define life.

Order

Organisms are highly organized structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex. Inside each cell, atoms make up molecules. These in turn make up cell

components or organelles. Multicellular organisms, which may consist of millions of individual cells, have an advantage over single-celled organisms in that their cells can be specialized to perform specific functions, and even sacrificed in certain situations for the good of the organism as a whole. How these specialized cells come together to form organs such as the heart, lung, or skin in organisms like the toad shown in [\[link\]](#) will be discussed later.



A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: "Ivengo(RUS)"/Wikimedia Commons)

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light or respond to touch ([\[link\]](#)). Even tiny bacteria can move toward or away from chemicals (a process called chemotaxis) or light (phototaxis). Movement toward a stimulus is considered a positive response, while movement away from a stimulus is considered a negative response.



The leaves of this sensitive plant (*Mimosa pudica*) will instantly droop and fold when touched. After a few minutes, the plant returns to its normal state. (credit: Alex Lomas)

Note:
Concept in Action



Watch this [video](#) to see how the sensitive plant responds to a touch stimulus.

Reproduction

Single-celled organisms reproduce by first duplicating their DNA, which is the genetic material, and then dividing it equally as the cell prepares to divide to form two new cells. Many multicellular organisms (those made up of more than one cell) produce specialized reproductive cells that will form new individuals. When reproduction occurs, DNA containing genes is passed along to an organism's offspring. These genes are the reason that the offspring will belong to the same species and will have characteristics similar to the parent, such as fur color and blood type.

Adaptation

All living organisms exhibit a “fit” to their environment. Biologists refer to this fit as adaptation and it is a consequence of evolution by natural selection, which operates in every lineage of reproducing organisms. Examples of adaptations are diverse and unique, from heat-resistant Archaea that live in boiling hot springs to the tongue length of a nectar-feeding moth that matches the size of the flower from which it feeds. All adaptations enhance the reproductive potential of the individual exhibiting them, including their ability to survive to reproduce. Adaptations are not constant. As an environment changes, natural selection causes the characteristics of the individuals in a population to track those changes.

Growth and Development

Organisms grow and develop according to specific instructions coded for by their genes. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young ([link](#)) will grow up to exhibit many of the same characteristics as its parents.



Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Pieter & Renée Lanser)

Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, such as the transport of nutrients, response to stimuli, and coping with environmental stresses. For example, organ systems such as the digestive or circulatory systems perform specific functions like carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis

To function properly, cells require appropriate conditions such as proper temperature, pH, and concentrations of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to

maintain internal conditions within a narrow range almost constantly, despite environmental changes, through a process called **homeostasis** or “steady state”—the ability of an organism to maintain constant internal conditions. For example, many organisms regulate their body temperature in a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear ([link](#)), have body structures that help them withstand low temperatures and conserve body heat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.



Polar bears and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin. (credit: "longhorndave"/Flickr)

Energy Processing

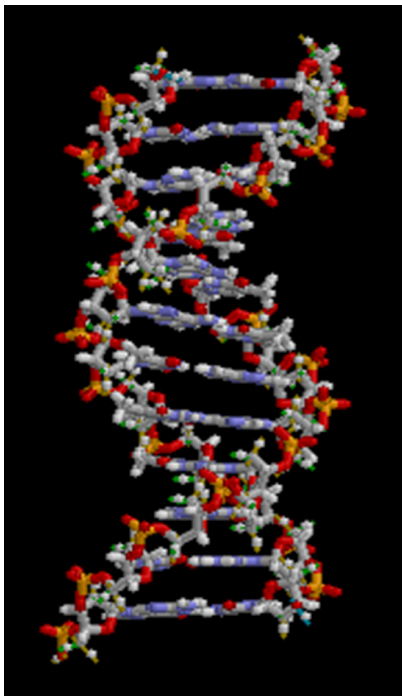
All organisms (such as the California condor shown in [\[link\]](#)) use a source of energy for their metabolic activities. Some organisms capture energy from the Sun and convert it into chemical energy in food; others use chemical energy from molecules they take in.



A lot of energy is required for a California condor to fly. Chemical energy derived from food is used to power flight. California condors are an endangered species; scientists have strived to place a wing tag on each bird to help them identify and locate each individual bird. (credit: Pacific Southwest Region U.S. Fish and Wildlife)

Levels of Organization of Living Things

Living things are highly organized and structured, following a hierarchy on a scale from small to large. The **atom** is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A **molecule** is a chemical structure consisting of at least two atoms held together by a chemical bond. Many molecules that are biologically important are **macromolecules**, large molecules that are typically formed by combining smaller units called monomers. An example of a macromolecule is deoxyribonucleic acid (DNA) ([link](#)), which contains the instructions for the functioning of the organism that contains it.



A molecule, like this large DNA molecule, is composed of atoms.

(credit:
"Brian0918"/Wikimedia Commons)

Note:

Concept in Action



To see an animation of this DNA molecule, click [here](#).

Some cells contain aggregates of macromolecules surrounded by membranes; these are called **organelles**. Organelles are small structures that exist within cells and perform specialized functions. All living things are made of cells; the **cell** itself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why viruses are not considered living: they are not made of cells. To make new viruses, they have to invade and hijack a living cell; only then can they obtain the materials they need to reproduce.) Some organisms consist of a single cell and others are multicellular. Cells are classified as prokaryotic or eukaryotic. **Prokaryotes** are single-celled organisms that lack organelles surrounded by a membrane and do not have nuclei surrounded by nuclear membranes; in contrast, the cells of **eukaryotes** do have membrane-bound organelles and nuclei.

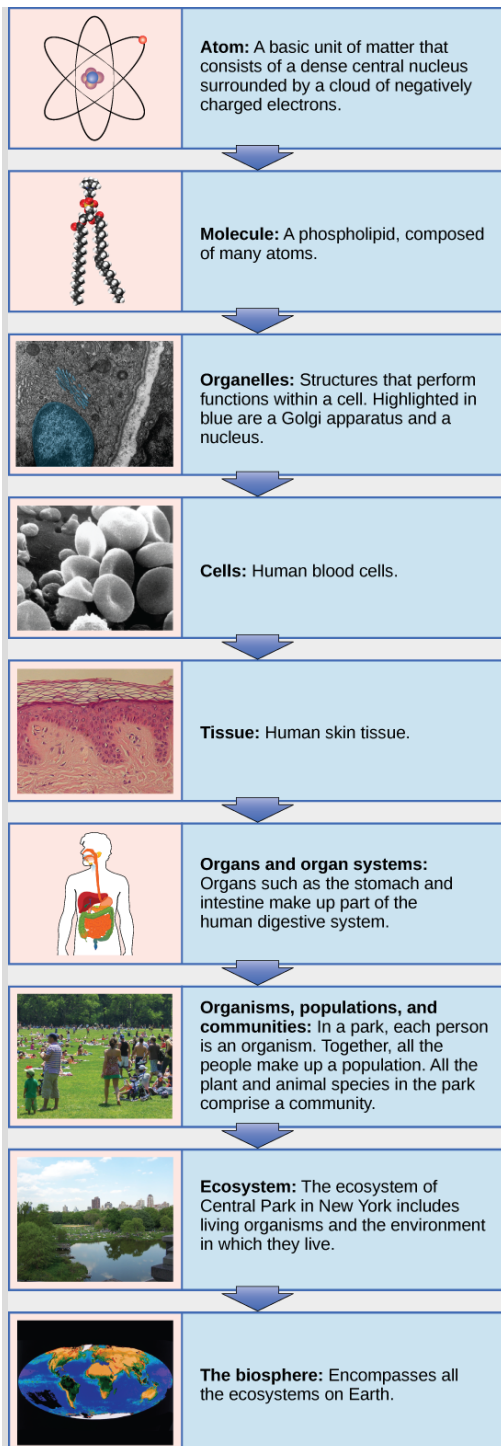
In most multicellular organisms, cells combine to make **tissues**, which are groups of similar cells carrying out the same function. **Organs** are collections of tissues grouped together based on a common function. Organs are present not only in animals but also in plants. An **organ system** is a higher level of organization that consists of functionally related organs. For example vertebrate animals have many organ systems, such as the

circulatory system that transports blood throughout the body and to and from the lungs; it includes organs such as the heart and blood vessels.

Organisms are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

Note:

Art Connection



From an atom to the entire Earth, biology examines all aspects of life. (credit "molecule": modification of work by

Jane Whitney; credit
"organelles":
modification of work by
Louisa Howard; credit
"cells": modification of
work by Bruce Wetzel,
Harry Schaefer, National
Cancer Institute; credit
"tissue": modification of
work by
"Kilbad"/Wikimedia
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Peter Dutton; credit
"ecosystem":
modification of work by
"gigi4791"/Flickr; credit
"biosphere": modification
of work by NASA)

Which of the following statements is false?

- a. Tissues exist within organs which exist within organ systems.
- b. Communities exist within populations which exist within ecosystems.
- c. Organelles exist within cells which exist within tissues.
- d. Communities exist within ecosystems which exist in the biosphere.

All the individuals of a species living within a specific area are collectively called a **population**. For example, a forest may include many white pine trees. All of these pine trees represent the population of white pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants and also insects and microbial populations. A **community** is the set of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. The forest itself is an ecosystem. An **ecosystem** consists of all the living things in a particular area together with the abiotic, or non-living, parts of that environment such as nitrogen in the soil or rainwater. At the highest level of organization ([\[link\]](#)), the **biosphere** is the collection of all ecosystems, and it represents the zones of life on Earth. It includes land, water, and portions of the atmosphere.

The Diversity of Life

The science of biology is very broad in scope because there is a tremendous diversity of life on Earth. The source of this diversity is **evolution**, the process of gradual change during which new species arise from older species. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

In the 18th century, a scientist named Carl Linnaeus first proposed organizing the known species of organisms into a hierarchical taxonomy. In this system, species that are most similar to each other are put together within a grouping known as a genus. Furthermore, similar genera (the plural of genus) are put together within a family. This grouping continues until all organisms are collected together into groups at the highest level. The current taxonomic system now has eight levels in its hierarchy, from lowest to highest, they are: species, genus, family, order, class, phylum, kingdom, domain. Thus species are grouped within genera, genera are grouped within families, families are grouped within orders, and so on ([\[link\]](#)).

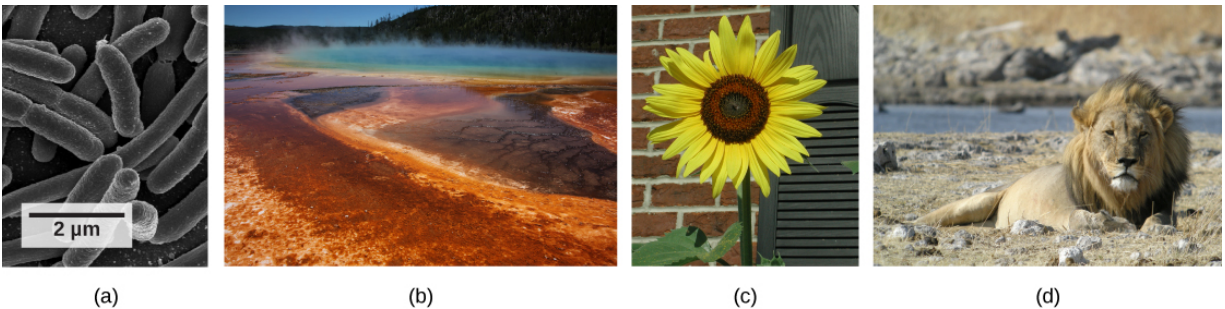
DOMAIN Eukarya	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat	Fish Snake	Earthworm Moth	Paramecium Tree
KINGDOM Animalia	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat	Fish Snake	Earthworm Moth	
PHYLUM Chordata	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat	Fish Snake		
CLASS Mammalia	Dog	Wolf	Coyote	Fox	Lion Seal	Mouse Human	Whale Bat			
ORDER Carnivora	Dog	Wolf	Coyote	Fox	Lion Seal					
FAMILY Canidae	Dog	Wolf	Coyote	Fox						
GENUS Canis	Dog	Wolf	Coyote							
SPECIES <i>Canis lupus</i>	Dog	Wolf								

This diagram shows the levels of taxonomic hierarchy for a dog, from the broadest category—domain—to the most specific—species.

The highest level, domain, is a relatively new addition to the system since the 1990s. Scientists now recognize three domains of life, the Eukarya, the Archaea, and the Bacteria. The domain Eukarya contains organisms that have cells with nuclei. It includes the kingdoms of fungi, plants, animals, and several kingdoms of protists. The Archaea, are single-celled organisms without nuclei and include many extremophiles that live in harsh environments like hot springs. The Bacteria are another quite different group of single-celled organisms without nuclei ([\[link\]](#)). Both the Archaea and the Bacteria are prokaryotes, an informal name for cells without nuclei. The recognition in the 1990s that certain “bacteria,” now known as the Archaea, were as different genetically and biochemically from other bacterial cells as they were from eukaryotes, motivated the recommendation to divide life into three domains. This dramatic change in our knowledge of the tree of life demonstrates that classifications are not permanent and will change when new information becomes available.

In addition to the hierarchical taxonomic system, Linnaeus was the first to name organisms using two unique names, now called the binomial naming system. Before Linnaeus, the use of common names to refer to organisms

caused confusion because there were regional differences in these common names. Binomial names consist of the genus name (which is capitalized) and the species name (all lower-case). Both names are set in italics when they are printed. Every species is given a unique binomial which is recognized the world over, so that a scientist in any location can know which organism is being referred to. For example, the North American blue jay is known uniquely as *Cyanocitta cristata*. Our own species is *Homo sapiens*.



These images represent different domains. The scanning electron micrograph shows (a) bacterial cells belong to the domain Bacteria, while the (b) extremophiles, seen all together as colored mats in this hot spring, belong to domain Archaea. Both the (c) sunflower and (d) lion are part of domain Eukarya. (credit a: modification of work by Rocky Mountain Laboratories, NIAID, NIH; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Frank Vassen)

Note:

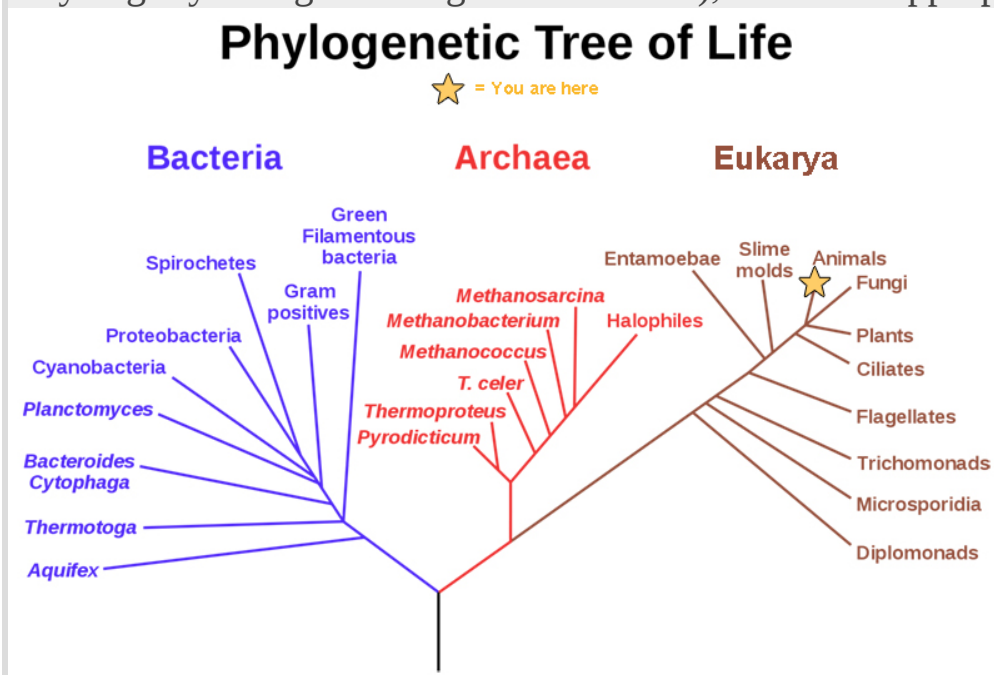
Evolution in Action

Carl Woese and the Phylogenetic Tree

The evolutionary relationships of various life forms on Earth can be summarized in a phylogenetic tree. A **phylogenetic tree** is a diagram showing the evolutionary relationships among biological species based on

similarities and differences in genetic or physical traits or both. A phylogenetic tree is composed of branch points, or nodes, and branches. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, an ancestor is thought to have diverged to form two new species. The length of each branch can be considered as estimates of relative time.

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. Woese proposed the domain as a new taxonomic level and Archaea as a new domain, to reflect the new phylogenetic tree ([\[link\]](#)). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape). Various genes were used in phylogenetic studies. Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, found in some slightly altered form in every organism, conserved (meaning that these genes have remained only slightly changed throughout evolution), and of an appropriate length.



This phylogenetic tree was constructed by microbiologist

Carl Woese using genetic relationships. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are organisms without a nucleus or other organelles surrounded by a membrane and, therefore, are prokaryotes. (credit: modification of work by Eric Gaba)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and sub disciplines. Biologists may pursue one of those sub disciplines and work in a more focused field. For instance, molecular biology studies biological processes at the molecular level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. Microbiology is the study of the structure and function of microorganisms. It is quite a broad branch itself, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Another field of biological study, neurobiology, studies the biology of the nervous system, and although it is considered a branch of biology, it is also recognized as an interdisciplinary field of study known as neuroscience. Because of its interdisciplinary nature, this sub discipline studies different functions of the nervous system using molecular, cellular, developmental, medical, and computational approaches.



Researchers work on excavating dinosaur fossils at a site in Castellón, Spain. (credit: Mario Modesto)

Paleontology, another branch of biology, uses fossils to study life's history ([link](#)). Zoology and botany are the study of animals and plants, respectively. Biologists can also specialize as biotechnologists, ecologists, or physiologists, to name just a few areas. Biotechnologists apply the knowledge of biology to create useful products. Ecologists study the interactions of organisms in their environments. Physiologists study the workings of cells, tissues and organs. This is just a small sample of the many fields that biologists can pursue. From our own bodies to the world we live in, discoveries in biology can affect us in very direct and important ways. We depend on these discoveries for our health, our food sources, and the benefits provided by our ecosystem. Because of this, knowledge of biology can benefit us in making decisions in our day-to-day lives.

The development of technology in the twentieth century that continues today, particularly the technology to describe and manipulate the genetic material, DNA, has transformed biology. This transformation will allow biologists to continue to understand the history of life in greater detail, how the human body works, our human origins, and how humans can survive as

a species on this planet despite the stresses caused by our increasing numbers. Biologists continue to decipher huge mysteries about life suggesting that we have only begun to understand life on the planet, its history, and our relationship to it. For this and other reasons, the knowledge of biology gained through this textbook and other printed and electronic media should be a benefit in whichever field you enter.

Note:**Careers in Action****Forensic Scientist**

Forensic science is the application of science to answer questions related to the law. Biologists as well as chemists and biochemists can be forensic scientists. Forensic scientists provide scientific evidence for use in courts, and their job involves examining trace material associated with crimes. Interest in forensic science has increased in the last few years, possibly because of popular television shows that feature forensic scientists on the job. Also, the development of molecular techniques and the establishment of DNA databases have updated the types of work that forensic scientists can do. Their job activities are primarily related to crimes against people such as murder, rape, and assault. Their work involves analyzing samples such as hair, blood, and other body fluids and also processing DNA ([\[link\]](#)) found in many different environments and materials. Forensic scientists also analyze other biological evidence left at crime scenes, such as insect parts or pollen grains. Students who want to pursue careers in forensic science will most likely be required to take chemistry and biology courses as well as some intensive math courses.



This forensic scientist works in a DNA extraction room at the U.S. Army Criminal Investigation Laboratory. (credit: U.S. Army CID Command Public Affairs)

Section Summary

Biology is the science of life. All living organisms share several key properties such as order, sensitivity or response to stimuli, reproduction, adaptation, growth and development, regulation, homeostasis, and energy processing. Living things are highly organized following a hierarchy that includes atoms, molecules, organelles, cells, tissues, organs, and organ systems. Organisms, in turn, are grouped as populations, communities, ecosystems, and the biosphere. Evolution is the source of the tremendous biological diversity on Earth today. A diagram called a phylogenetic tree can be used to show evolutionary relationships among organisms. Biology is very broad and includes many branches and sub disciplines. Examples

include molecular biology, microbiology, neurobiology, zoology, and botany, among others.

Art Connections

Exercise:

Problem: [\[link\]](#) Which of the following statements is false?

- A. Tissues exist within organs which exist within organ systems.
- B. Communities exist within populations which exist within ecosystems.
- C. Organelles exist within cells which exist within tissues.
- D. Communities exist within ecosystems which exist in the biosphere.

Solution:

[\[link\]](#) B

Multiple Choice

Exercise:

Problem:

The smallest unit of biological structure that meets the functional requirements of “living” is the _____.

- a. organ
- b. organelle
- c. cell
- d. macromolecule

Solution:

C

Exercise:

Problem:

Which of the following sequences represents the hierarchy of biological organization from the most complex to the least complex level?

- a. organelle, tissue, biosphere, ecosystem, population
- b. organ, organism, tissue, organelle, molecule
- c. organism, community, biosphere, molecule, tissue, organ
- d. biosphere, ecosystem, community, population, organism

Solution:

D

Free Response

Exercise:

Problem:

Using examples, explain how biology can be studied from a microscopic approach to a global approach.

Solution:

Researchers can approach biology from the smallest to the largest, and everything in between. For instance, an ecologist may study a population of individuals, the population's community, the community's ecosystem, and the ecosystem's part in the biosphere. When studying an individual organism, a biologist could examine the cell and its organelles, the tissues that the cells make up, the organs and their respective organ systems, and the sum total—the organism itself.

Glossary

atom

a basic unit of matter that cannot be broken down by normal chemical reactions

biology

the study of living organisms and their interactions with one another and their environments

biosphere

a collection of all ecosystems on Earth

cell

the smallest fundamental unit of structure and function in living things

community

a set of populations inhabiting a particular area

ecosystem

all living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote

an organism with cells that have nuclei and membrane-bound organelles

evolution

the process of gradual change in a population that can also lead to new species arising from older species

homeostasis

the ability of an organism to maintain constant internal conditions

macromolecule

a large molecule typically formed by the joining of smaller molecules

molecule

a chemical structure consisting of at least two atoms held together by a chemical bond

organ

a structure formed of tissues operating together to perform a common function

organ system

the higher level of organization that consists of functionally related organs

organelle

a membrane-bound compartment or sac within a cell

organism

an individual living entity

phylogenetic tree

a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both

population

all individuals within a species living within a specific area

prokaryote

a unicellular organism that lacks a nucleus or any other membrane-bound organelle

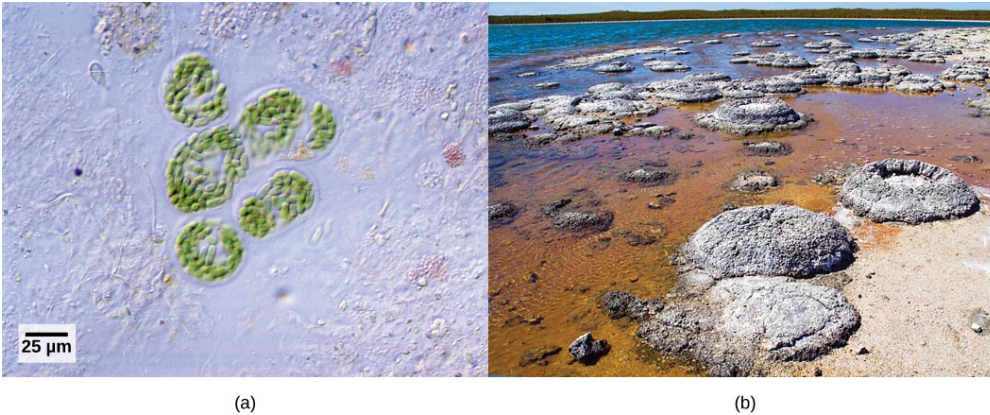
tissue

a group of similar cells carrying out the same function

The Process of Science

By the end of this section, you will be able to:

- Identify the shared characteristics of the natural sciences
- Understand the process of scientific inquiry
- Compare inductive reasoning with deductive reasoning
- Describe the goals of basic science and applied science



Formerly called blue-green algae, the (a) cyanobacteria seen through a light microscope are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by the layering of cyanobacteria in shallow waters. (credit a: modification of work by NASA; scale-bar data from Matt Russell; credit b: modification of work by Ruth Ellison)

Like geology, physics, and chemistry, biology is a science that gathers knowledge about the natural world. Specifically, biology is the study of life. The discoveries of biology are made by a community of researchers who work individually and together using agreed-on methods. In this sense, biology, like all sciences is a social enterprise like politics or the arts. The methods of science include careful observation, record keeping, logical and mathematical reasoning, experimentation, and submitting conclusions to the scrutiny of others. Science also requires considerable imagination and

creativity; a well-designed experiment is commonly described as elegant, or beautiful. Like politics, science has considerable practical implications and some science is dedicated to practical applications, such as the prevention of disease (see [\[link\]](#)). Other science proceeds largely motivated by curiosity. Whatever its goal, there is no doubt that science, including biology, has transformed human existence and will continue to do so.



Biologists may choose to study *Escherichia coli* (*E. coli*), a bacterium that is a normal resident of our digestive tracts but which is also sometimes responsible for disease outbreaks. In this micrograph, the bacterium is visualized using a scanning electron microscope and digital colorization. (credit: Eric Erbe; digital colorization by Christopher Pooley, USDA-ARS)

The Nature of Science

Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? **Science** (from the Latin

scientia, meaning "knowledge") can be defined as knowledge about the natural world.

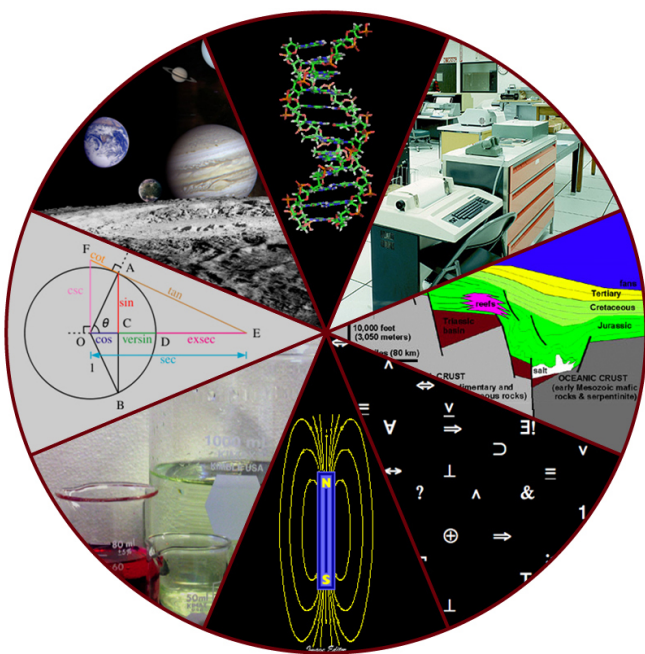
Science is a very specific way of learning, or knowing, about the world. The history of the past 500 years demonstrates that science is a very powerful way of knowing about the world; it is largely responsible for the technological revolutions that have taken place during this time. There are however, areas of knowledge and human experience that the methods of science cannot be applied to. These include such things as answering purely moral questions, aesthetic questions, or what can be generally categorized as spiritual questions. Science cannot investigate these areas because they are outside the realm of material phenomena, the phenomena of matter and energy, and cannot be observed and measured.

The **scientific method** is a method of research with defined steps that include experiments and careful observation. The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses. A **hypothesis** is a suggested explanation for an event, which can be tested. Hypotheses, or tentative explanations, are generally produced within the context of a **scientific theory**. A scientific theory is a generally accepted, thoroughly tested and confirmed explanation for a set of observations or phenomena. Scientific theory is the foundation of scientific knowledge. In addition, in many scientific disciplines (less so in biology) there are **scientific laws**, often expressed in mathematical formulas, which describe how elements of nature will behave under certain specific conditions. There is not an evolution of hypotheses through theories to laws as if they represented some increase in certainty about the world. Hypotheses are the day-to-day material that scientists work with and they are developed within the context of theories. Laws are concise descriptions of parts of the world that are amenable to formulaic or mathematical description.

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A

planetarium? Gems and minerals? Or maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics ([\[link\]](#)). However, those fields of science related to the physical world and its phenomena and processes are considered **natural sciences**. Thus, a museum of natural sciences might contain any of the items listed above.



Some fields of science include astronomy, biology, computer science, geology, logic, physics, chemistry, and mathematics.
(credit: "Image Editor"/Flickr)

There is no complete agreement when it comes to defining what the natural sciences include. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into **life sciences**, which study living things and include biology, and **physical sciences**, which study nonliving matter and

include astronomy, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on two sciences and are interdisciplinary.

Scientific Inquiry

One thing is common to all forms of science: an ultimate goal “to know.” Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. Two methods of logical thinking are used: inductive reasoning and deductive reasoning.

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative (descriptive) or quantitative (consisting of numbers), and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies often work this way. Many brains are observed while people are doing a task. The part of the brain that lights up, indicating activity, is then demonstrated to be the part controlling the response to that task.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reasoning, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. **Deductive reasoning** is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. For example, a prediction would be that if the climate is becoming warmer in a region, the distribution of plants and animals should change. Comparisons have been made between distributions in the past and the present, and the many changes that have been found are consistent with a warming climate. Finding the change in distribution is evidence that the climate change conclusion is a valid one.

Both types of logical thinking are related to the two main pathways of scientific study: descriptive science and hypothesis-based science.

Descriptive (or discovery) **science** aims to observe, explore, and discover, while **hypothesis-based science** begins with a specific question or problem and a potential answer or solution that can be tested. The boundary between these two forms of study is often blurred, because most scientific endeavors combine both approaches. Observations lead to questions, questions lead to forming a hypothesis as a possible answer to those questions, and then the hypothesis is tested. Thus, descriptive science and hypothesis-based science are in continuous dialogue.

Hypothesis Testing

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific method was used even in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626) ([\[link\]](#)), who set up inductive methods for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost anything as a logical problem-solving method.



Sir Francis Bacon
is credited with
being the first to
document the
scientific method.

The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, "The classroom is warm because no one turned on the air conditioning." But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be,

“The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, a prediction may be made. A prediction is similar to a hypothesis but it typically has the format “If . . . then” For example, the prediction for the first hypothesis might be, “*If the student turns on the air conditioning, then the classroom will no longer be too warm.*”

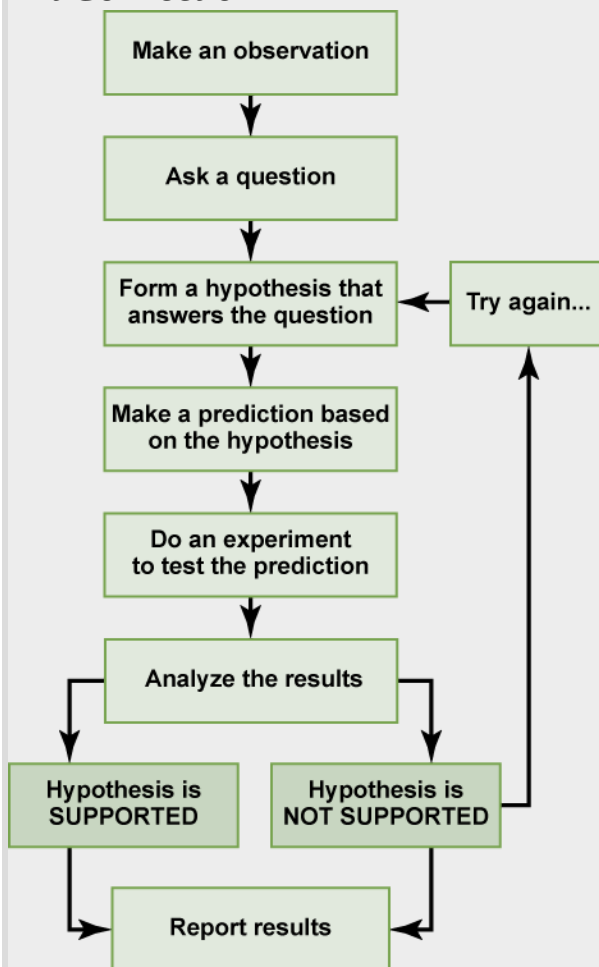
A hypothesis must be testable to ensure that it is valid. For example, a hypothesis that depends on what a bear thinks is not testable, because it can never be known what a bear thinks. It should also be **falsifiable**, meaning that it can be disproven by experimental results. An example of an unfalsifiable hypothesis is “Botticelli’s *Birth of Venus* is beautiful.” There is no experiment that might show this statement to be false. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. This is important. A hypothesis can be disproven, or eliminated, but it can never be proven. Science does not deal in proofs like mathematics. If an experiment fails to disprove a hypothesis, then we find support for that explanation, but this is not to say that down the road a better explanation will not be found, or a more carefully designed experiment will be found to falsify the hypothesis.

Each experiment will have one or more variables and one or more controls. A **variable** is any part of the experiment that can vary or change during the experiment. A **control** is a part of the experiment that does not change. Look for the variables and controls in the example that follows. As a simple example, an experiment might be conducted to test the hypothesis that phosphate limits the growth of algae in freshwater ponds. A series of artificial ponds are filled with water and half of them are treated by adding phosphate each week, while the other half are treated by adding a salt that is known not to be used by algae. The variable here is the phosphate (or lack of phosphate), the experimental or treatment cases are the ponds with added phosphate and the control ponds are those with something inert added, such as the salt. Just adding something is also a control against the possibility that adding extra matter to the pond has an effect. If the treated ponds show lesser growth of algae, then we have found support for our hypothesis. If

they do not, then we reject our hypothesis. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid ([link](#)). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

Note:

Art Connection



The scientific method is a series of defined steps that include experiments and careful observation. If a hypothesis is

not supported by data, a new hypothesis can be proposed.

In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn't toast my bread.
2. Why doesn't my toaster work?
3. There is something wrong with the electrical outlet.
4. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
5. I plug my coffeemaker into the outlet.
6. My coffeemaker works.

In practice, the scientific method is not as rigid and structured as it might at first appear. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests.

Basic and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or bettering our lives? This question focuses on the differences between two types of science: basic science and applied science.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on

developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge's sake, though this does not mean that in the end it may not result in an application.

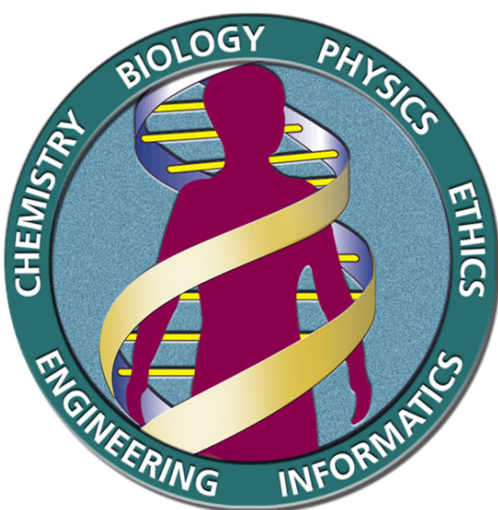
In contrast, **applied science** or “technology,” aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster. In applied science, the problem is usually defined for the researcher.

Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the knowledge generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, new copies of DNA are made, shortly before a cell divides to form new cells. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits

and the exact location of each gene. (The gene is the basic unit of heredity; an individual's complete collection of genes is his or her genome.) Other organisms have also been studied as part of this project to gain a better understanding of human chromosomes. The Human Genome Project ([link](#)) relied on basic research carried out with non-human organisms and, later, with the human genome. An important end goal eventually became using the data for applied research seeking cures for genetically related diseases.



The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science.

The project was completed in 2003.

(credit: the U.S. Department of Energy Genome Programs)

While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by serendipity, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings for other researchers to expand and build upon their discoveries. Communication and collaboration within and between sub disciplines of science are key to the advancement of knowledge in science. For this reason, an important aspect of a scientist's work is disseminating results and communicating with peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the limited few who are present. Instead, most scientists present their results in peer-reviewed articles that are published in scientific journals. **Peer-reviewed articles** are scientific papers that are reviewed, usually anonymously by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of peer review helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

There are many journals and the popular press that do not use a peer-review system. A large number of online open-access journals, journals with articles available without cost, are now available many of which use rigorous peer-review systems, but some of which do not. Results of any

studies published in these forums without peer review are not reliable and should not form the basis for other scientific work. In one exception, journals may allow a researcher to cite a personal communication from another researcher about unpublished results with the cited author's permission.

Section Summary

Biology is the science that studies living organisms and their interactions with one another and their environments. Science attempts to describe and understand the nature of the universe in whole or in part. Science has many fields; those fields related to the physical world and its phenomena are considered natural sciences.

A hypothesis is a tentative explanation for an observation. A scientific theory is a well-tested and consistently verified explanation for a set of observations or phenomena. A scientific law is a description, often in the form of a mathematical formula, of the behavior of an aspect of nature under certain circumstances. Two types of logical reasoning are used in science. Inductive reasoning uses results to produce general scientific principles. Deductive reasoning is a form of logical thinking that predicts results by applying general principles. The common thread throughout scientific research is the use of the scientific method. Scientists present their results in peer-reviewed scientific papers published in scientific journals.

Science can be basic or applied. The main goal of basic science is to expand knowledge without any expectation of short-term practical application of that knowledge. The primary goal of applied research, however, is to solve practical problems.

Art Connections

Exercise:

Problem:

[\[link\]](#) In the example below, the scientific method is used to solve an everyday problem. Which part in the example below is the hypothesis? Which is the prediction? Based on the results of the experiment, is the hypothesis supported? If it is not supported, propose some alternative hypotheses.

1. My toaster doesn't toast my bread.
 2. Why doesn't my toaster work?
 3. There is something wrong with the electrical outlet.
 4. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
 5. I plug my coffeemaker into the outlet.
 6. My coffeemaker works.
-

Solution:

[\[link\]](#) The hypothesis is #3 (there is something wrong with the electrical outlet), and the prediction is #4 (if something is wrong with the outlet, then the coffeemaker also won't work when plugged into the outlet). The original hypothesis is not supported, as the coffee maker works when plugged into the outlet. Alternative hypotheses may include (1) the toaster might be broken or (2) the toaster wasn't turned on.

Multiple Choice**Exercise:****Problem:**

A suggested and testable explanation for an event is called a _____.

- a. hypothesis

- b. variable
- c. theory
- d. control

Solution:

A

Exercise:

Problem:

The type of logical thinking that uses related observations to arrive at a general conclusion is called _____.

- a. deductive reasoning
- b. the scientific method
- c. hypothesis-based science
- d. inductive reasoning

Solution:

D

Free Response

Exercise:

Problem:

Give an example of how applied science has had a direct effect on your daily life.

Solution:

Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to

prevent diseases such as polio, measles, tetanus, and even the influenza affect daily life by contributing to individual and societal health.

Glossary

applied science

a form of science that solves real-world problems

basic science

science that seeks to expand knowledge regardless of the short-term application of that knowledge

control

a part of an experiment that does not change during the experiment

deductive reasoning

a form of logical thinking that uses a general statement to forecast specific results

descriptive science

a form of science that aims to observe, explore, and find things out

falsifiable

able to be disproven by experimental results

hypothesis

a suggested explanation for an event, which can be tested

hypothesis-based science

a form of science that begins with a specific explanation that is then tested

inductive reasoning

a form of logical thinking that uses related observations to arrive at a general conclusion

life science

a field of science, such as biology, that studies living things

natural science

a field of science that studies the physical world, its phenomena, and processes

peer-reviewed article

a scientific report that is reviewed by a scientist's colleagues before publication

physical science

a field of science, such as astronomy, physics, and chemistry, that studies nonliving matter

science

knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific law

a description, often in the form of a mathematical formula, for the behavior of some aspect of nature under certain specific conditions

scientific method

a method of research with defined steps that include experiments and careful observation

scientific theory

a thoroughly tested and confirmed explanation for observations or phenomena

variable

a part of an experiment that can vary or change

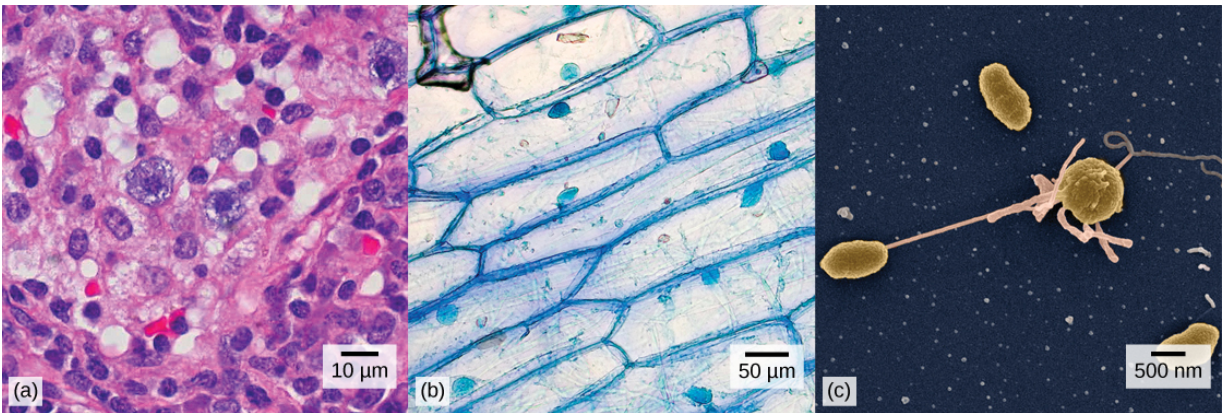
Introduction

class="introduction"

(a) Nasal
sinus cells
(viewed with
a light
microscope),
(b) onion
cells (viewed
with a light
microscope),
and (c) *Vibrio
tasmaniensis*
bacterial cells
(viewed using
a scanning
electron
microscope)
are from very
different
organisms,
yet all share
certain
characteristic
s of basic cell
structure.

(credit a:
modification
of work by
Ed Uthman,
MD; credit b:
modification
of work by
Umberto
Salvagnin;
credit c:

modification
of work by
Anthony
D'Onofrio;
scale-bar data
from Matt
Russell)



Close your eyes and picture a brick wall. What is the basic building block of that wall? It is a single brick, of course. Like a brick wall, your body is composed of basic building blocks, and the building blocks of your body are cells.

Your body has many kinds of cells, each specialized for a specific purpose. Just as a home is made from a variety of building materials, the human body is constructed from many cell types. For example, epithelial cells protect the surface of the body and cover the organs and body cavities within. Bone cells help to support and protect the body. Cells of the immune system fight invading bacteria. Additionally, red blood cells carry oxygen throughout the body. Each of these cell types plays a vital role during the growth, development, and day-to-day maintenance of the body. In spite of their enormous variety, however, all cells share certain fundamental characteristics.

How Cells Are Studied

By the end of this section, you will be able to:

- Describe the roles of cells in organisms
- Compare and contrast light microscopy and electron microscopy
- Summarize the cell theory

A cell is the smallest unit of a living thing. A living thing, like you, is called an organism. Thus, cells are the basic building blocks of all organisms.

In multicellular organisms, several cells of one particular kind interconnect with each other and perform shared functions to form tissues (for example, muscle tissue, connective tissue, and nervous tissue), several tissues combine to form an organ (for example, stomach, heart, or brain), and several organs make up an organ system (such as the digestive system, circulatory system, or nervous system). Several systems functioning together form an organism (such as an elephant, for example).

There are many types of cells, and all are grouped into one of two broad categories: prokaryotic and eukaryotic. Animal cells, plant cells, fungal cells, and protist cells are classified as eukaryotic, whereas bacteria and archaea cells are classified as prokaryotic. Before discussing the criteria for determining whether a cell is prokaryotic or eukaryotic, let us first examine how biologists study cells.

Microscopy

Cells vary in size. With few exceptions, individual cells are too small to be seen with the naked eye, so scientists use microscopes to study them. A **microscope** is an instrument that magnifies an object. Most images of cells are taken with a microscope and are called micrographs.

Light Microscopes

To give you a sense of the size of a cell, a typical human red blood cell is about eight millionths of a meter or eight micrometers (abbreviated as μm)

in diameter; the head of a pin is about two thousandths of a meter (millimeters, or mm) in diameter. That means that approximately 250 red blood cells could fit on the head of a pin.

The optics of the lenses of a light microscope changes the orientation of the image. A specimen that is right-side up and facing right on the microscope slide will appear upside-down and facing left when viewed through a microscope, and vice versa. Similarly, if the slide is moved left while looking through the microscope, it will appear to move right, and if moved down, it will seem to move up. This occurs because microscopes use two sets of lenses to magnify the image. Due to the manner in which light travels through the lenses, this system of lenses produces an inverted image (binoculars and a dissecting microscope work in a similar manner, but include an additional magnification system that makes the final image appear to be upright).

Most student microscopes are classified as light microscopes ([link](#)a). Visible light both passes through and is bent by the lens system to enable the user to see the specimen. Light microscopes are advantageous for viewing living organisms, but since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells.

Light microscopes commonly used in the undergraduate college laboratory magnify up to approximately 400 times. Two parameters that are important in microscopy are magnification and resolving power. Magnification is the degree of enlargement of an object. Resolving power is the ability of a microscope to allow the eye to distinguish two adjacent structures as separate; the higher the resolution, the closer those two objects can be, and the better the clarity and detail of the image. When oil immersion lenses are used, magnification is usually increased to 1,000 times for the study of smaller cells, like most prokaryotic cells. Because light entering a specimen from below is focused onto the eye of an observer, the specimen can be viewed using light microscopy. For this reason, for light to pass through a specimen, the sample must be thin or translucent.

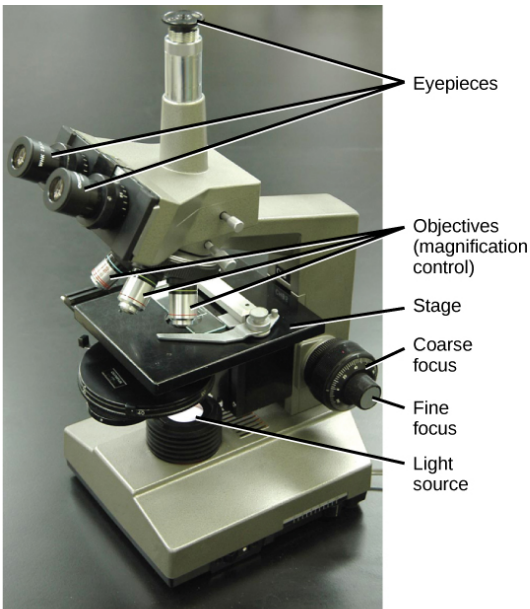
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Concept in Action

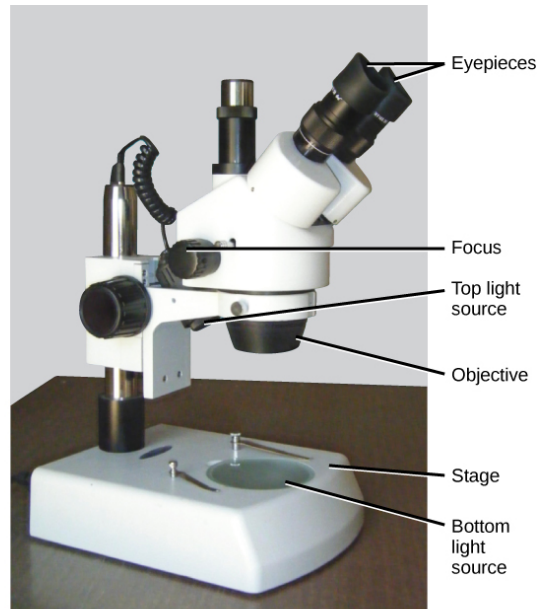


For another perspective on cell size, try the [HowBig](#) interactive.

A second type of microscope used in laboratories is the dissecting microscope ([link](#)**b**). These microscopes have a lower magnification (20 to 80 times the object size) than light microscopes and can provide a three-dimensional view of the specimen. Thick objects can be examined with many components in focus at the same time. These microscopes are designed to give a magnified and clear view of tissue structure as well as the anatomy of the whole organism. Like light microscopes, most modern dissecting microscopes are also binocular, meaning that they have two separate lens systems, one for each eye. The lens systems are separated by a certain distance, and therefore provide a sense of depth in the view of their subject to make manipulations by hand easier. Dissecting microscopes also have optics that correct the image so that it appears as if being seen by the naked eye and not as an inverted image. The light illuminating a sample under a dissecting microscope typically comes from above the sample, but may also be directed from below.



(a)



(b)

(a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times. (b) Dissecting microscopes have a lower magnification than light microscopes and are used to examine larger objects, such as tissues.

Electron Microscopes

In contrast to light microscopes, electron microscopes use a beam of electrons instead of a beam of light. Not only does this allow for higher magnification and, thus, more detail ([\[link\]](#)), it also provides higher resolving power. Preparation of a specimen for viewing under an electron microscope will kill it; therefore, live cells cannot be viewed using this type of microscopy. In addition, the electron beam moves best in a vacuum, making it impossible to view living materials.

In a scanning electron microscope, a beam of electrons moves back and forth across a cell's surface, rendering the details of cell surface characteristics by reflection. Cells and other structures are usually coated

with a metal like gold. In a transmission electron microscope, the electron beam is transmitted through the cell and provides details of a cell's internal structures. As you might imagine, electron microscopes are significantly more bulky and expensive than are light microscopes.



- (a) *Salmonella* bacteria are viewed with a light microscope.
- (b) This scanning electron micrograph shows *Salmonella* bacteria (in red) invading human cells. (credit a: modification of work by CDC, Armed Forces Institute of Pathology, Charles N. Farmer; credit b: modification of work by Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell)

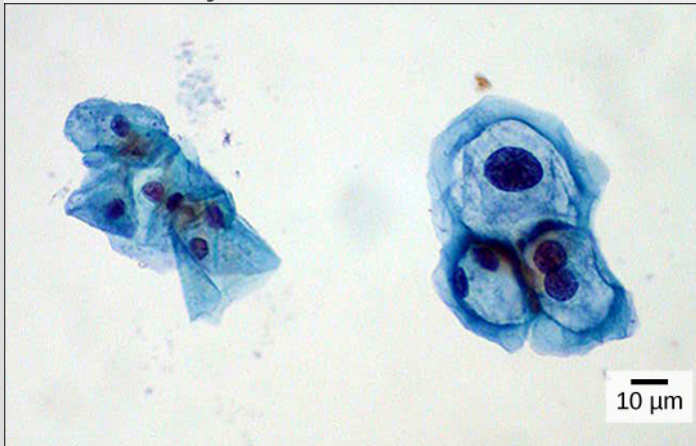
Note:

Careers in Action

Cytotechnologist

Have you ever heard of a medical test called a Pap smear ([\[link\]](#))? In this test, a doctor takes a small sample of cells from the uterine cervix of a patient and sends it to a medical lab where a cytotechnologist stains the cells and examines them for any changes that could indicate cervical cancer or a microbial infection.

Cytotechnologists (*cyto-* = cell) are professionals who study cells through microscopic examinations and other laboratory tests. They are trained to determine which cellular changes are within normal limits or are abnormal. Their focus is not limited to cervical cells; they study cellular specimens that come from all organs. When they notice abnormalities, they consult a pathologist, who is a medical doctor who can make a clinical diagnosis. Cytotechnologists play vital roles in saving people's lives. When abnormalities are discovered early, a patient's treatment can begin sooner, which usually increases the chances of successful treatment.



These uterine cervix cells, viewed through a light microscope, were obtained from a Pap smear. Normal cells are on the left. The cells on the right are infected with human papillomavirus. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Cell Theory

The microscopes we use today are far more complex than those used in the 1600s by Antony van Leeuwenhoek, a Dutch shopkeeper who had great

skill in crafting lenses. Despite the limitations of his now-ancient lenses, van Leeuwenhoek observed the movements of protists (a type of single-celled organism) and sperm, which he collectively termed “animalcules.”

In a 1665 publication called *Micrographia*, experimental scientist Robert Hooke coined the term “cell” (from the Latin *cella*, meaning “small room”) for the box-like structures he observed when viewing cork tissue through a lens. In the 1670s, van Leeuwenhoek discovered bacteria and protozoa. Later advances in lenses and microscope construction enabled other scientists to see different components inside cells.

By the late 1830s, botanist Matthias Schleiden and zoologist Theodor Schwann were studying tissues and proposed the **unified cell theory**, which states that all living things are composed of one or more cells, that the cell is the basic unit of life, and that all new cells arise from existing cells. These principles still stand today.

Section Summary

A cell is the smallest unit of life. Most cells are so small that they cannot be viewed with the naked eye. Therefore, scientists must use microscopes to study cells. Electron microscopes provide higher magnification, higher resolution, and more detail than light microscopes. The unified cell theory states that all organisms are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells.

Multiple Choice

Exercise:

Problem:

When viewing a specimen through a light microscope, scientists use _____ to distinguish the individual components of cells.

- a. a beam of electrons
- b. radioactive isotopes

- c. special stains
 - d. high temperatures
-

Solution:

C

Exercise:

Problem: The _____ is the basic unit of life.

- a. organism
 - b. cell
 - c. tissue
 - d. organ
-

Solution:

B

Free Response

Exercise:

Problem:

What are the advantages and disadvantages of light, transmission, and scanning electron microscopes?

Solution:

The advantages of light microscopes are that they are easily obtained, and the light beam does not kill the cells. However, typical light microscopes are somewhat limited in the amount of detail that they can reveal. Electron microscopes are ideal because you can view intricate details, but they are bulky and costly, and preparation for the

microscopic examination kills the specimen. Transmission electron microscopes are designed to examine the internal structures of a cell, whereas a scanning electron microscope only allows visualization of the surface of a structure.

Glossary

microscope

the instrument that magnifies an object

unified cell theory

the biological concept that states that all organisms are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells

Comparing Prokaryotic and Eukaryotic Cells

By the end of this section, you will be able to:

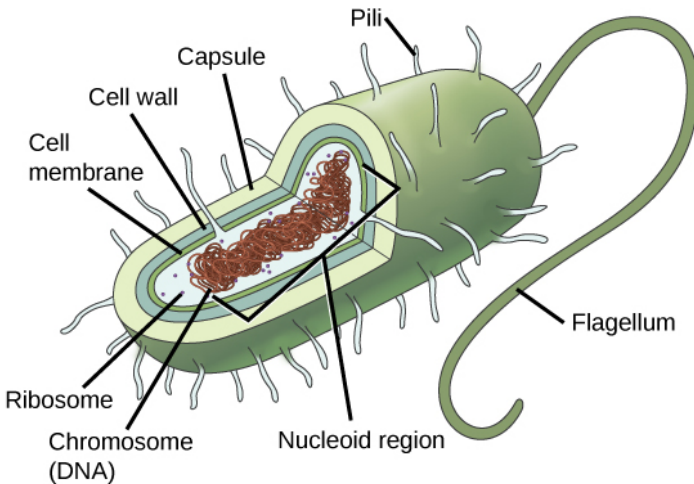
- Name examples of prokaryotic and eukaryotic organisms
- Compare and contrast prokaryotic cells and eukaryotic cells
- Describe the relative sizes of different kinds of cells

Cells fall into one of two broad categories: prokaryotic and eukaryotic. The predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (*pro-* = before; *-karyon-* = nucleus). Animal cells, plant cells, fungi, and protists are eukaryotes (*eu-* = true).

Components of Prokaryotic Cells

All cells share four common components: 1) a plasma membrane, an outer covering that separates the cell's interior from its surrounding environment; 2) cytoplasm, consisting of a jelly-like region within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, particles that synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

A **prokaryotic cell** is a simple, single-celled (unicellular) organism that lacks a nucleus, or any other membrane-bound organelle. We will shortly come to see that this is significantly different in eukaryotes. Prokaryotic DNA is found in the central part of the cell: a darkened region called the nucleoid ([link](#)).



This figure shows the generalized structure of a prokaryotic cell.

Unlike Archaea and eukaryotes, bacteria have a cell wall made of peptidoglycan, comprised of sugars and amino acids, and many have a polysaccharide capsule ([\[link\]](#)). The cell wall acts as an extra layer of protection, helps the cell maintain its shape, and prevents dehydration. The capsule enables the cell to attach to surfaces in its environment. Some prokaryotes have flagella, pili, or fimbriae. Flagella are used for locomotion, while most pili are used to exchange genetic material during a type of reproduction called conjugation.

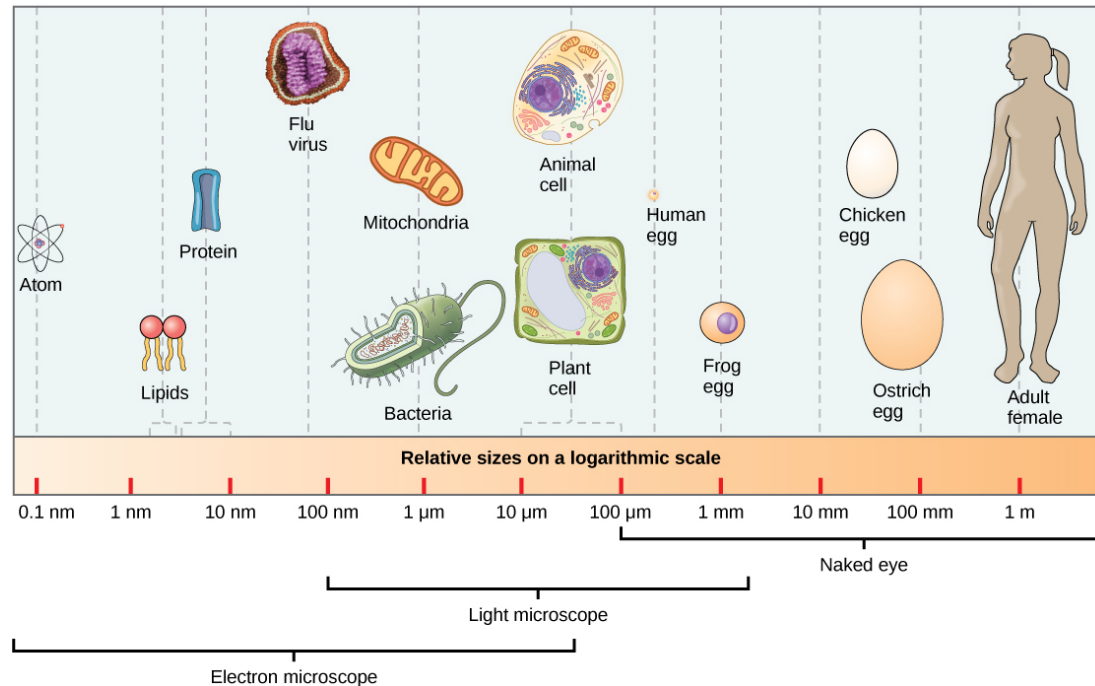
Eukaryotic Cells

In nature, the relationship between form and function is apparent at all levels, including the level of the cell, and this will become clear as we explore eukaryotic cells. The principle “form follows function” is found in many contexts. For example, birds and fish have streamlined bodies that allow them to move quickly through the medium in which they live, be it air or water. It means that, in general, one can deduce the function of a structure by looking at its form, because the two are matched.

A **eukaryotic cell** is a cell that has a membrane-bound nucleus and other membrane-bound compartments or sacs, called **organelles**, which have specialized functions. The word eukaryotic means “true kernel” or “true nucleus,” alluding to the presence of the membrane-bound nucleus in these cells. The word “organelle” means “little organ,” and, as already mentioned, organelles have specialized cellular functions, just as the organs of your body have specialized functions.

Cell Size

At 0.1–5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10–100 μm ([\[link\]](#)). The small size of prokaryotes allows ions and organic molecules that enter them to quickly spread to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly move out. However, larger eukaryotic cells have evolved different structural adaptations to enhance cellular transport. Indeed, the large size of these cells would not be possible without these adaptations. In general, cell size is limited because volume increases much more quickly than does cell surface area. As a cell becomes larger, it becomes more and more difficult for the cell to acquire sufficient materials to support the processes inside the cell, because the relative size of the surface area across which materials must be transported declines.



This figure shows the relative sizes of different kinds of cells and cellular components. An adult human is shown for comparison.

Section Summary

Prokaryotes are predominantly single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, a cell wall, DNA, and lack membrane-bound organelles. Many also have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1–5.0 μm .

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. Eukaryotic cells tend to be 10 to 100 times the size of prokaryotic cells.

Multiple Choice

Exercise:

Problem: Which of these do all prokaryotes and eukaryotes share?

- a. nuclear envelope
- b. cell walls
- c. organelles
- d. plasma membrane

Solution:

D

Exercise:

Problem:

A typical prokaryotic cell _____ compared to a eukaryotic cell.

- a. is smaller in size by a factor of 100
- b. is similar in size
- c. is smaller in size by a factor of one million
- d. is larger in size by a factor of 10

Solution:

A

Free Response

Exercise:

Problem:

Describe the structures that are characteristic of a prokaryote cell.

Solution:

Prokaryotic cells are surrounded by a plasma membrane and have DNA, cytoplasm, and ribosomes, like eukaryotic cells. They also have cell walls and may have a cell capsule. Prokaryotes have a single large chromosome that is not surrounded by a nuclear membrane.

Prokaryotes may have flagella or motility, pili for conjugation, and fimbriae for adhesion to surfaces.

Glossary

eukaryotic cell

a cell that has a membrane-bound nucleus and several other membrane-bound compartments or sacs

organelle

a membrane-bound compartment or sac within a cell

prokaryotic cell

a unicellular organism that lacks a nucleus or any other membrane-bound organelle

Eukaryotic Cells

By the end of this section, you will be able to:

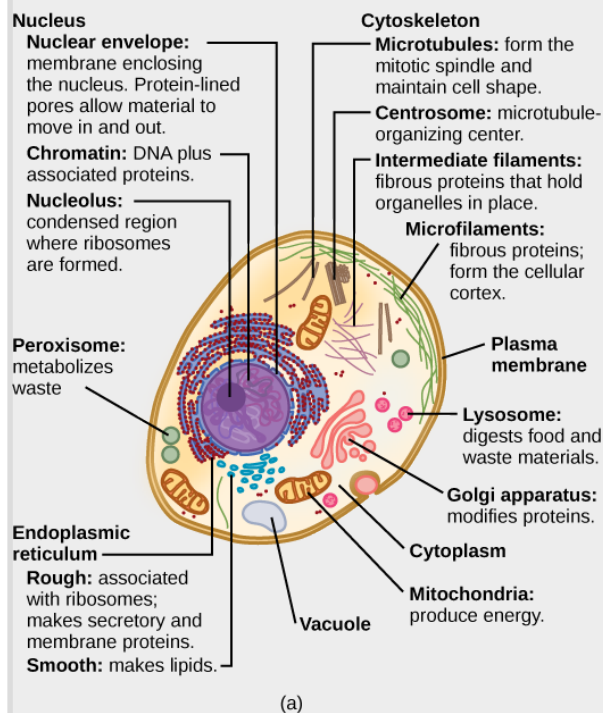
- Describe the structure of eukaryotic plant and animal cells
- State the role of the plasma membrane
- Summarize the functions of the major cell organelles
- Describe the cytoskeleton and extracellular matrix

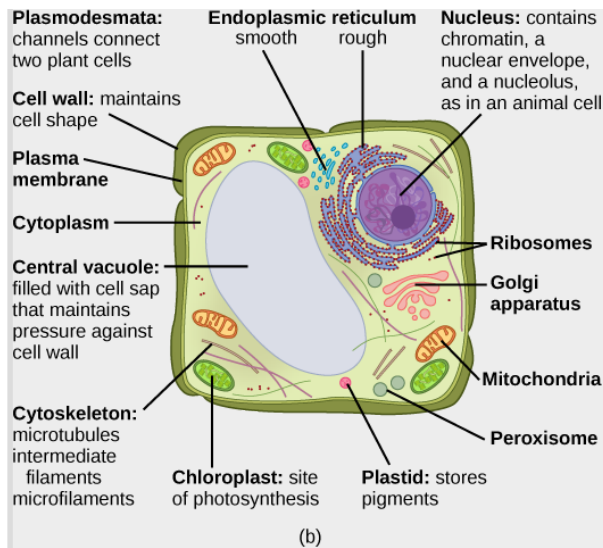
At this point, it should be clear that eukaryotic cells have a more complex structure than do prokaryotic cells. Organelles allow for various functions to occur in the cell at the same time. Before discussing the functions of organelles within a eukaryotic cell, let us first examine two important components of the cell: the plasma membrane and the cytoplasm.

Note:

Art Connection

This figure shows (a) a typical animal cell and (b) a typical plant cell.

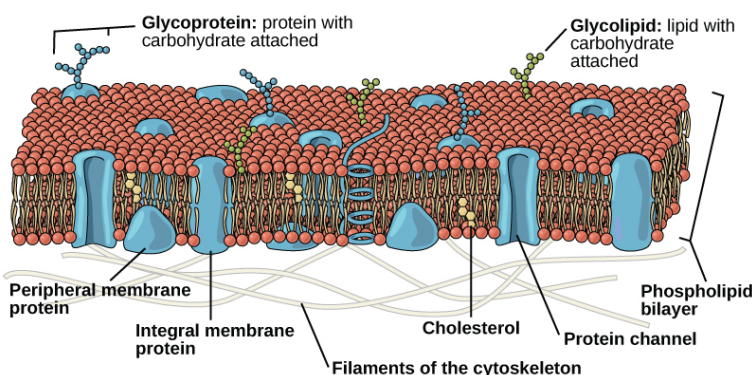




What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a **plasma membrane** ([link](#)) made up of a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule composed of two fatty acid chains, a glycerol backbone, and a phosphate group. The plasma membrane regulates the passage of some substances, such as organic molecules, ions, and water, preventing the passage of some to maintain internal conditions, while actively bringing in or removing others. Other compounds move passively across the membrane.



The plasma membrane is a phospholipid bilayer with embedded proteins. There are other components, such as cholesterol and

carbohydrates, which can be found in the membrane in addition to phospholipids and protein.

The plasma membranes of cells that specialize in absorption are folded into fingerlike projections called microvilli (singular = microvillus). This folding increases the surface area of the plasma membrane. Such cells are typically found lining the small intestine, the organ that absorbs nutrients from digested food. This is an excellent example of form matching the function of a structure.

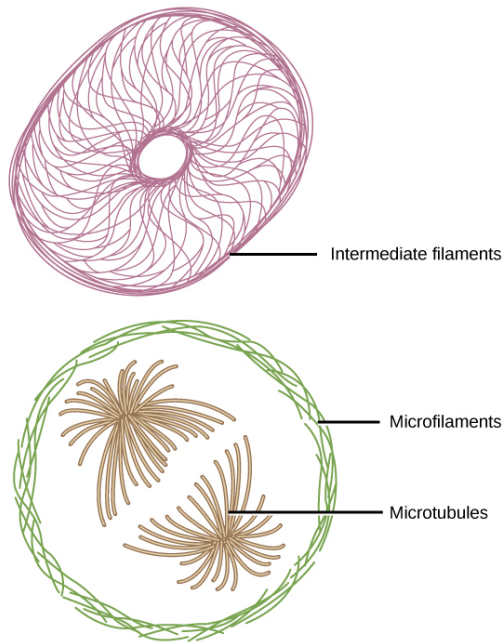
People with celiac disease have an immune response to gluten, which is a protein found in wheat, barley, and rye. The immune response damages microvilli, and thus, afflicted individuals cannot absorb nutrients. This leads to malnutrition, cramping, and diarrhea. Patients suffering from celiac disease must follow a gluten-free diet.

The Cytoplasm

The **cytoplasm** comprises the contents of a cell between the plasma membrane and the nuclear envelope (a structure to be discussed shortly). It is made up of organelles suspended in the gel-like **cytosol**, the cytoskeleton, and various chemicals ([\[link\]](#)). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules found in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are found there too. Ions of sodium, potassium, calcium, and many other elements are also dissolved in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

The Cytoskeleton

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that helps to maintain the shape of the cell, secures certain organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently. Collectively, this network of protein fibers is known as the **cytoskeleton**. There are three types of fibers within the cytoskeleton: microfilaments, also known as actin filaments, intermediate filaments, and microtubules ([\[link\]](#)).



Microfilaments, intermediate filaments, and microtubules compose a cell's cytoskeleton.

Microfilaments are the thinnest of the cytoskeletal fibers and function in moving cellular components, for example, during cell division. They also maintain the structure of microvilli, the extensive folding of the plasma membrane found in cells dedicated to absorption. These components are also common in muscle cells and are responsible for muscle cell contraction. Intermediate filaments are of intermediate diameter and have structural functions, such as maintaining the shape of the cell and anchoring organelles. Keratin, the compound that strengthens hair and nails, forms one type of intermediate filament. Microtubules are the thickest of the cytoskeletal fibers. These are hollow tubes that can dissolve and reform quickly. Microtubules guide organelle movement and are the structures that pull chromosomes to their poles during cell division. They are also the structural components of flagella and cilia. In cilia and flagella, the microtubules are organized as a circle of nine double microtubules on the outside and two microtubules in the center.

The centrosome is a region near the nucleus of animal cells that functions as a microtubule-organizing center. It contains a pair of centrioles, two structures that lie perpendicular to each other. Each centriole is a cylinder of nine triplets of microtubules.

The centrosome replicates itself before a cell divides, and the centrioles play a role in pulling the duplicated chromosomes to opposite ends of the dividing cell. However, the exact function of the centrioles in cell division is not clear, since cells that have the

centrioles removed can still divide, and plant cells, which lack centrioles, are capable of cell division.

Flagella and Cilia

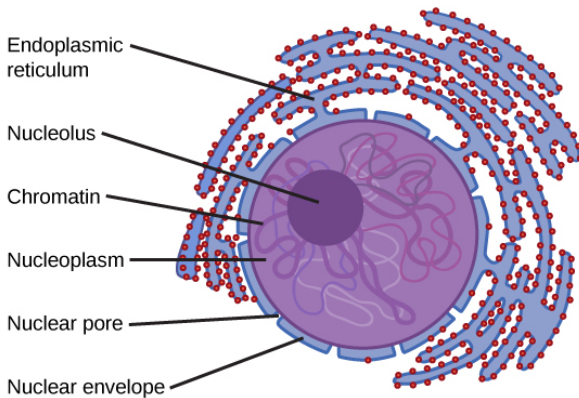
Flagella (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move an entire cell, (for example, sperm, *Euglena*). When present, the cell has just one flagellum or a few flagella. When **cilia** (singular = cilium) are present, however, they are many in number and extend along the entire surface of the plasma membrane. They are short, hair-like structures that are used to move entire cells (such as paramecium) or move substances along the outer surface of the cell (for example, the cilia of cells lining the fallopian tubes that move the ovum toward the uterus, or cilia lining the cells of the respiratory tract that move particulate matter toward the throat that mucus has trapped).

The Endomembrane System

The **endomembrane system** (*endo* = within) is a group of membranes and organelles ([\[link\]](#)) in eukaryotic cells that work together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles.

The Nucleus

Typically, the nucleus is the most prominent organelle in a cell ([\[link\]](#)). The **nucleus** (plural = nuclei) houses the cell's DNA in the form of chromatin and directs the synthesis of ribosomes and proteins. Let us look at it in more detail ([\[link\]](#)).



The outermost boundary of the nucleus is the nuclear envelope. Notice that the nuclear envelope consists of two phospholipid bilayers (membranes)—an outer membrane and an inner membrane—in contrast to the plasma membrane ([link](#)), which consists of only one phospholipid bilayer. (credit: modification of work by NIGMS, NIH)

The **nuclear envelope** is a double-membrane structure that constitutes the outermost portion of the nucleus ([link](#)). Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers.

The nuclear envelope is punctuated with pores that control the passage of ions, molecules, and RNA between the nucleoplasm and the cytoplasm.

To understand chromatin, it is helpful to first consider chromosomes. Chromosomes are structures within the nucleus that are made up of DNA, the hereditary material, and proteins. This combination of DNA and proteins is called chromatin. In eukaryotes, chromosomes are linear structures. Every species has a specific number of chromosomes in the nucleus of its body cells. For example, in humans, the chromosome number is 46, whereas in fruit flies, the chromosome number is eight.

Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, the chromosomes resemble an unwound, jumbled bunch of threads.

We already know that the nucleus directs the synthesis of ribosomes, but how does it do this? Some chromosomes have sections of DNA that encode ribosomal RNA. A darkly staining area within the nucleus, called the **nucleolus** (plural = nucleoli), aggregates the ribosomal RNA with associated proteins to assemble the ribosomal subunits that are then transported through the nuclear pores into the cytoplasm.

The Endoplasmic Reticulum

The **endoplasmic reticulum (ER)** ([link](#)) is a series of interconnected membranous tubules that collectively modify proteins and synthesize lipids. However, these two functions are performed in separate areas of the endoplasmic reticulum: the rough endoplasmic reticulum and the smooth endoplasmic reticulum, respectively.

The hollow portion of the ER tubules is called the lumen or cisternal space. The membrane of the ER, which is a phospholipid bilayer embedded with proteins, is continuous with the nuclear envelope.

The **rough endoplasmic reticulum (RER)** is so named because the ribosomes attached to its cytoplasmic surface give it a studded appearance when viewed through an electron microscope.

The ribosomes synthesize proteins while attached to the ER, resulting in transfer of their newly synthesized proteins into the lumen of the RER where they undergo modifications such as folding or addition of sugars. The RER also makes phospholipids for cell membranes.

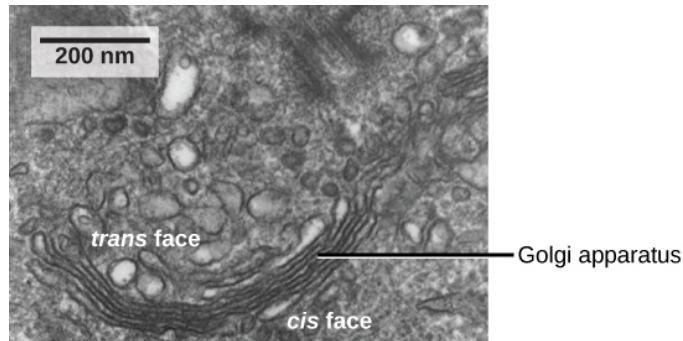
If the phospholipids or modified proteins are not destined to stay in the RER, they will be packaged within vesicles and transported from the RER by budding from the membrane ([link](#)). Since the RER is engaged in modifying proteins that will be secreted from the cell, it is abundant in cells that secrete proteins, such as the liver.

The **smooth endoplasmic reticulum (SER)** is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (see [link](#)). The SER's functions include synthesis of carbohydrates, lipids (including phospholipids), and steroid hormones; detoxification of medications and poisons; alcohol metabolism; and storage of calcium ions.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles need to be sorted, packaged, and tagged so that they wind up in the right place. The sorting, tagging, packaging, and distribution of lipids and proteins take place in the

Golgi apparatus (also called the Golgi body), a series of flattened membranous sacs ([link](#)).



The Golgi apparatus in this transmission electron micrograph of a white blood cell is visible as a stack of semicircular flattened rings in the lower portion of this image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell)

The Golgi apparatus has a receiving face near the endoplasmic reticulum and a releasing face on the side away from the ER, toward the cell membrane. The transport vesicles that form from the ER travel to the receiving face, fuse with it, and empty their contents into the lumen of the Golgi apparatus. As the proteins and lipids travel through the Golgi, they undergo further modifications. The most frequent modification is the addition of short chains of sugar molecules. The newly modified proteins and lipids are then tagged with small molecular groups to enable them to be routed to their proper destinations.

Finally, the modified and tagged proteins are packaged into vesicles that bud from the opposite face of the Golgi. While some of these vesicles, transport vesicles, deposit their contents into other parts of the cell where they will be used, others, secretory vesicles, fuse with the plasma membrane and release their contents outside the cell.

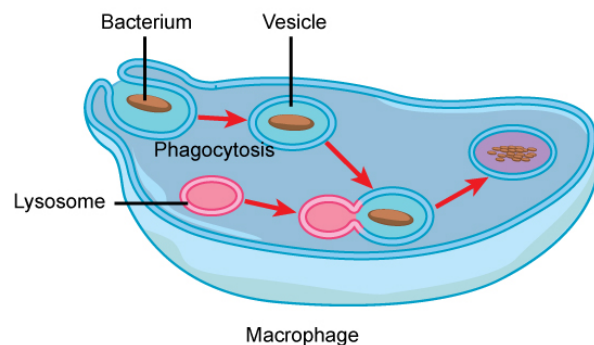
The amount of Golgi in different cell types again illustrates that form follows function within cells. Cells that engage in a great deal of secretory activity (such as cells of the salivary glands that secrete digestive enzymes or cells of the immune system that secrete antibodies) have an abundant number of Golgi.

In plant cells, the Golgi has an additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which are used in other parts of the cell.

Lysosomes

In animal cells, the **lysosomes** are the cell's "garbage disposal." Digestive enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. In single-celled eukaryotes, lysosomes are important for digestion of the food they ingest and the recycling of organelles. These enzymes are active at a much lower pH (more acidic) than those located in the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, thus the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Lysosomes also use their hydrolytic enzymes to destroy disease-causing organisms that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body's immune system. In a process known as phagocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome's hydrolytic enzymes then destroy the pathogen ([link](#)).



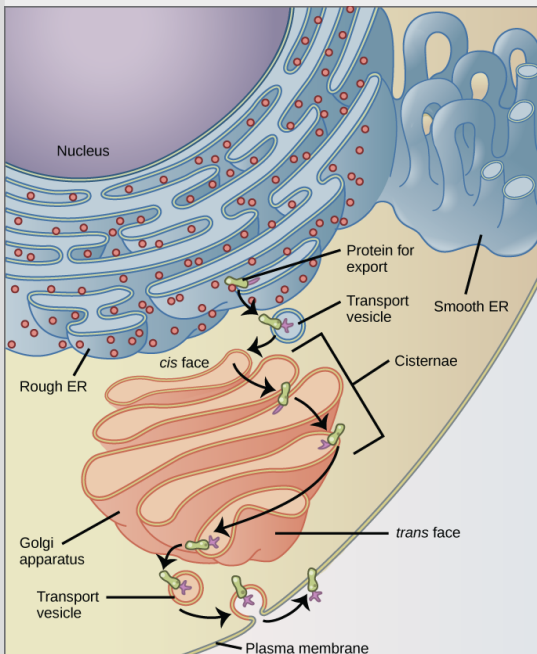
A macrophage has phagocytized a potentially pathogenic bacterium into a vesicle, which then fuses with a lysosome within the cell so that the pathogen can be destroyed. Other organelles are present in the cell, but for simplicity, are not shown.

Vesicles and Vacuoles

Vesicles and **vacuoles** are membrane-bound sacs that function in storage and transport. Vacuoles are somewhat larger than vesicles, and the membrane of a vacuole does not fuse with the membranes of other cellular components. Vesicles can fuse with other membranes within the cell system. Additionally, enzymes within plant vacuoles can break down macromolecules.

Note:

Art Connection



The endomembrane system works to modify, package, and transport lipids and proteins. (credit: modification of work by Magnus Manske)

Why does the *cis* face of the Golgi not face the plasma membrane?

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis. When viewed through an electron microscope, free ribosomes appear as either clusters or single tiny dots

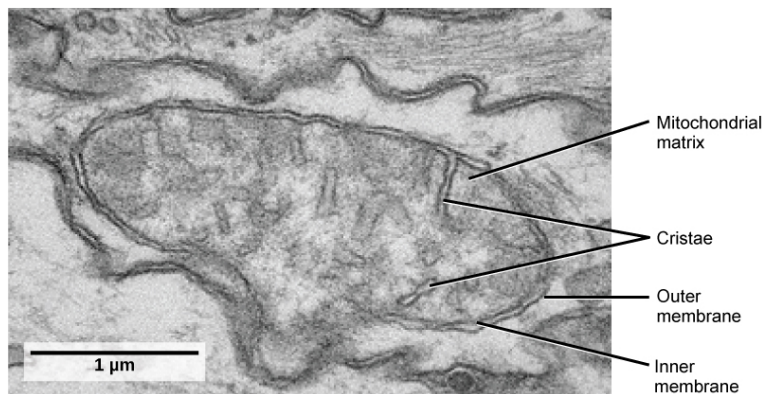
floating freely in the cytoplasm. Ribosomes may be attached to either the cytoplasmic side of the plasma membrane or the cytoplasmic side of the endoplasmic reticulum ([\[link\]](#)). Electron microscopy has shown that ribosomes consist of large and small subunits. Ribosomes are enzyme complexes that are responsible for protein synthesis.

Because protein synthesis is essential for all cells, ribosomes are found in practically every cell, although they are smaller in prokaryotic cells. They are particularly abundant in immature red blood cells for the synthesis of hemoglobin, which functions in the transport of oxygen throughout the body.

Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main energy-carrying molecule. The formation of ATP from the breakdown of glucose is known as cellular respiration. Mitochondria are oval-shaped, double-membrane organelles ([\[link\]](#)) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae, which increase the surface area of the inner membrane. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

In keeping with our theme of form following function, it is important to point out that muscle cells have a very high concentration of mitochondria because muscle cells need a lot of energy to contract.



This transmission electron micrograph shows a mitochondrion as viewed with an electron microscope. Notice the inner and outer membranes, the cristae, and the mitochondrial matrix. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Peroxisomes

Peroxisomes are small, round organelles enclosed by single membranes. They carry out oxidation reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. Alcohol is detoxified by peroxisomes in liver cells. A byproduct of these oxidation reactions is hydrogen peroxide, H_2O_2 , which is contained within the peroxisomes to prevent the chemical from causing damage to cellular components outside of the organelle. Hydrogen peroxide is safely broken down by peroxisomal enzymes into water and oxygen.

Animal Cells versus Plant Cells

Despite their fundamental similarities, there are some striking differences between animal and plant cells (see [\[link\]](#)). Animal cells have centrioles, centrosomes (discussed under the cytoskeleton), and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts, plasmodesmata, and plastids used for storage, and a large central vacuole, whereas animal cells do not.

The Cell Wall

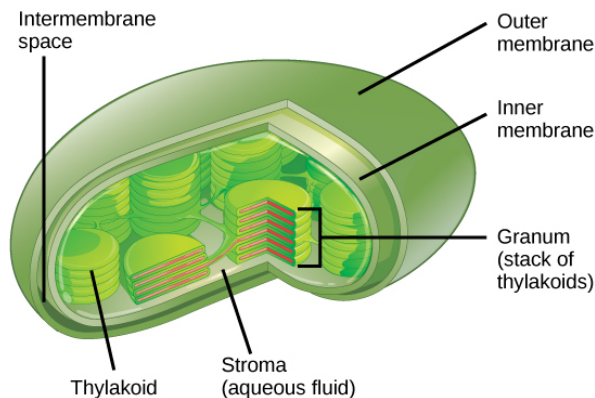
In [\[link\]](#), the diagram of a plant cell, you see a structure external to the plasma membrane called the cell wall. The **cell wall** is a rigid covering that protects the cell, provides structural support, and gives shape to the cell. Fungal and protist cells also have cell walls.

While the chief component of prokaryotic cell walls is peptidoglycan, the major organic molecule in the plant cell wall is cellulose, a polysaccharide made up of long, straight chains of glucose units. When nutritional information refers to dietary fiber, it is referring to the cellulose content of food.

Chloroplasts

Like mitochondria, chloroplasts also have their own DNA and ribosomes. **Chloroplasts** function in photosynthesis and can be found in eukaryotic cells such as plants and algae. In photosynthesis, carbon dioxide, water, and light energy are used to make glucose and oxygen. This is the major difference between plants and animals: Plants (autotrophs) are able to make their own food, like glucose, whereas animals (heterotrophs) must rely on other organisms for their organic compounds or food source.

Like mitochondria, chloroplasts have outer and inner membranes, but within the space enclosed by a chloroplast's inner membrane is a set of interconnected and stacked, fluid-filled membrane sacs called thylakoids ([link](#)). Each stack of thylakoids is called a granum (plural = grana). The fluid enclosed by the inner membrane and surrounding the grana is called the stroma.



This simplified diagram of a chloroplast shows the outer membrane, inner membrane, thylakoids, grana, and stroma.

The chloroplasts contain a green pigment called chlorophyll, which captures the energy of sunlight for photosynthesis. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria also perform photosynthesis, but they do not have chloroplasts. Their photosynthetic pigments are located in the thylakoid membrane within the cell itself.

Note:**Evolution in Action****Endosymbiosis**

We have mentioned that both mitochondria and chloroplasts contain DNA and ribosomes. Have you wondered why? Strong evidence points to endosymbiosis as the explanation. Symbiosis is a relationship in which organisms from two separate species live in close association and typically exhibit specific adaptations to each other. Endosymbiosis (*endo* = within) is a relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. Microbes that produce vitamin K live inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and are provided a stable habitat and abundant food by living within the large intestine.

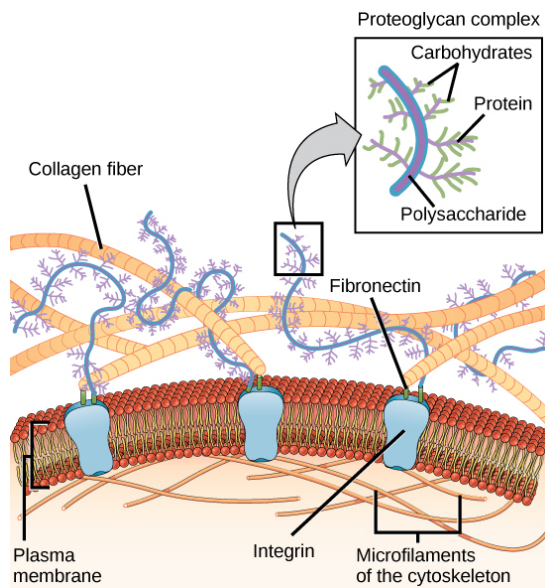
Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that mitochondria and chloroplasts have DNA and ribosomes, just as bacteria do. Scientists believe that host cells and bacteria formed a mutually beneficial endosymbiotic relationship when the host cells ingested aerobic bacteria and cyanobacteria but did not destroy them. Through evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the photosynthetic bacteria becoming chloroplasts.

The Central Vacuole

Previously, we mentioned vacuoles as essential components of plant cells. If you look at [\[link\]](#), you will see that plant cells each have a large, central vacuole that occupies most of the cell. The **central vacuole** plays a key role in regulating the cell's concentration of water in changing environmental conditions. In plant cells, the liquid inside the central vacuole provides turgor pressure, which is the outward pressure caused by the fluid inside the cell. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That is because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm and into the soil. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of a plant results in the wilted appearance. Additionally, this fluid has a very bitter taste, which discourages consumption by insects and animals. The central vacuole also functions to store proteins in developing seed cells.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are glycoproteins and the protein collagen. Collectively, these materials are called the **extracellular matrix** ([\[link\]](#)). Not only does the extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other.



The extracellular matrix consists of a network of substances secreted by cells.

Blood clotting provides an example of the role of the extracellular matrix in cell communication. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel, stimulates adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel), and initiates a series of steps that stimulate the platelets to produce clotting factors.

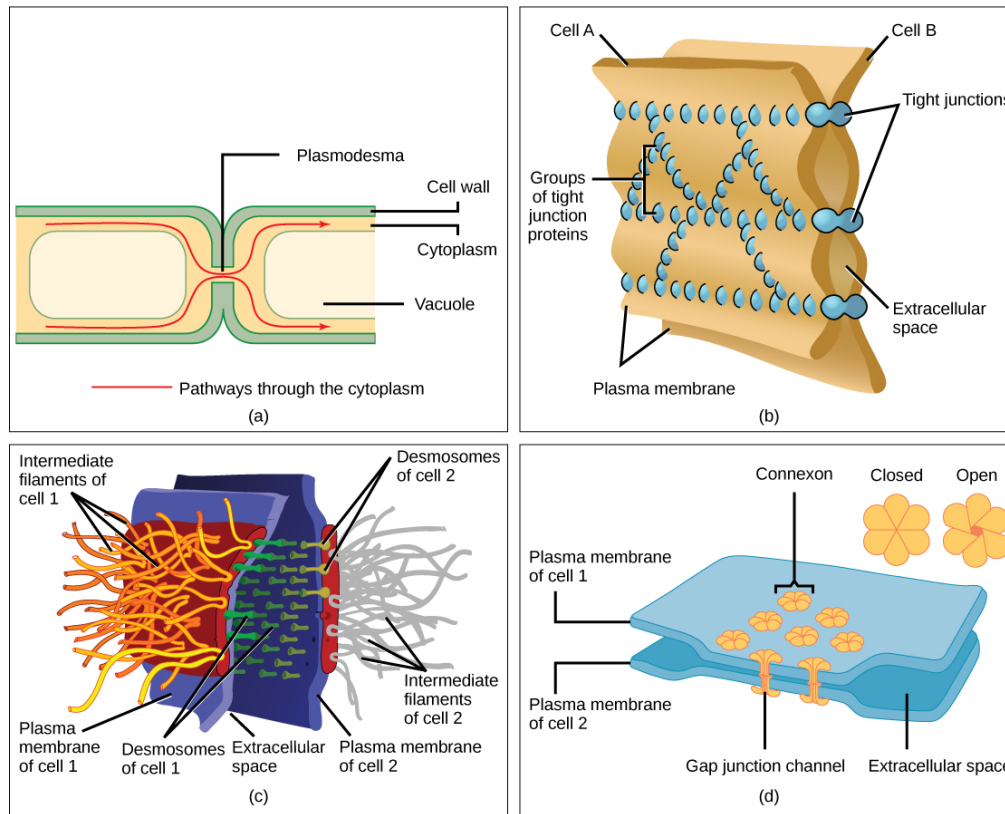
Intercellular Junctions

Cells can also communicate with each other by direct contact, referred to as intercellular junctions. There are some differences in the ways that plant and animal cells do this.

Plasmodesmata (singular = plasmodesma) are junctions between plant cells, whereas animal cell contacts include tight and gap junctions, and desmosomes.

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell walls surrounding each cell.

Plasmodesmata are numerous channels that pass between the cell walls of adjacent plant cells, connecting their cytoplasm and enabling signal molecules and nutrients to be transported from cell to cell ([link](#)).



There are four kinds of connections between cells. (a) A plasmodesma is a channel between the cell walls of two adjacent plant cells. (b) Tight junctions join adjacent animal cells. (c) Desmosomes join two animal cells together. (d) Gap junctions act as channels between animal cells. (credit b, c, d: modification of work by Mariana Ruiz Villareal)

A **tight junction** is a watertight seal between two adjacent animal cells ([link](#)b). Proteins hold the cells tightly against each other. This tight adhesion prevents materials from leaking between the cells. Tight junctions are typically found in the epithelial tissue that lines internal organs and cavities, and composes most of the skin. For example, the tight junctions of the epithelial cells lining the urinary bladder prevent urine from leaking into the extracellular space.

Also found only in animal cells are **desmosomes**, which act like spot welds between adjacent epithelial cells ([link](#)c). They keep cells together in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other

substances that enable cells to communicate ([link](#)d). Structurally, however, gap junctions and plasmodesmata differ.

Components of Prokaryotic and Eukaryotic Cells and Their Functions				
Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from external environment; controls passage of organic molecules, ions, water, oxygen, and wastes into and out of the cell	Yes	Yes	Yes
Cytoplasm	Provides structure to cell; site of many metabolic reactions; medium in which organelles are found	Yes	Yes	Yes
Nucleoid	Location of DNA	Yes	No	No
Nucleus	Cell organelle that houses DNA and directs synthesis of ribosomes and proteins	No	Yes	Yes
Ribosomes	Protein synthesis	Yes	Yes	Yes

Components of Prokaryotic and Eukaryotic Cells and Their Functions				
Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Mitochondria	ATP production/cellular respiration	No	Yes	Yes
Peroxisomes	Oxidizes and breaks down fatty acids and amino acids, and detoxifies poisons	No	Yes	Yes
Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes
Centrosome	Unspecified role in cell division in animal cells; organizing center of microtubules in animal cells	No	Yes	No
Lysosomes	Digestion of macromolecules; recycling of worn-out organelles	No	Yes	No
Cell wall	Protection, structural support and maintenance of cell shape	Yes, primarily peptidoglycan in bacteria but not Archaea	No	Yes, primarily cellulose
Chloroplasts	Photosynthesis	No	No	Yes

Components of Prokaryotic and Eukaryotic Cells and Their Functions				
Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Endoplasmic reticulum	Modifies proteins and synthesizes lipids	No	Yes	Yes
Golgi apparatus	Modifies, sorts, tags, packages, and distributes lipids and proteins	No	Yes	Yes
Cytoskeleton	Maintains cell's shape, secures organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move independently	Yes	Yes	Yes
Flagella	Cellular locomotion	Some	Some	No, except for some plant sperm.
Cilia	Cellular locomotion, movement of particles along extracellular surface of plasma membrane, and filtration	No	Some	No

This table provides the components of prokaryotic and eukaryotic cells and their respective functions.

Section Summary

Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. The plasma membrane is a phospholipid bilayer embedded with proteins. The nucleolus within the nucleus is the site for ribosome assembly. Ribosomes are found in the cytoplasm or are attached to the cytoplasmic side of the plasma membrane or endoplasmic reticulum. They perform protein synthesis. Mitochondria perform cellular respiration and produce ATP. Peroxisomes break down fatty acids, amino acids, and some toxins. Vesicles and vacuoles are storage and transport compartments. In plant cells, vacuoles also help break down macromolecules.

Animal cells also have a centrosome and lysosomes. The centrosome has two bodies, the centrioles, with an unknown role in cell division. Lysosomes are the digestive organelles of animal cells.

Plant cells have a cell wall, chloroplasts, and a central vacuole. The plant cell wall, whose primary component is cellulose, protects the cell, provides structural support, and gives shape to the cell. Photosynthesis takes place in chloroplasts. The central vacuole expands, enlarging the cell without the need to produce more cytoplasm.

The endomembrane system includes the nuclear envelope, the endoplasmic reticulum, Golgi apparatus, lysosomes, vesicles, as well as the plasma membrane. These cellular components work together to modify, package, tag, and transport membrane lipids and proteins.

The cytoskeleton has three different types of protein elements. Microfilaments provide rigidity and shape to the cell, and facilitate cellular movements. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression, serve as tracks for motor proteins that move vesicles through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. They are also the structural elements of centrioles, flagella, and cilia.

Animal cells communicate through their extracellular matrices and are connected to each other by tight junctions, desmosomes, and gap junctions. Plant cells are connected and communicate with each other by plasmodesmata.

Art Connections

Exercise:

Problem:

[\[link\]](#) What structures does a plant cell have that an animal cell does not have? What structures does an animal cell have that a plant cell does not have?

Solution:

[\[link\]](#) Plant cells have plasmodesmata, a cell wall, a large central vacuole, chloroplasts, and plastids. Animal cells have lysosomes and centrosomes.

Exercise:

Problem: [\[link\]](#) Why does the *cis* face of the Golgi not face the plasma membrane?

Solution:

[\[link\]](#) Because that face receives chemicals from the ER, which is toward the center of the cell.

Multiple Choice**Exercise:**

Problem: Which of the following is found both in eukaryotic and prokaryotic cells?

- a. nucleus
- b. mitochondrion
- c. vacuole
- d. ribosome

Solution:

D

Exercise:

Problem: Which of the following is not a component of the endomembrane system?

- a. mitochondrion
 - b. Golgi apparatus
 - c. endoplasmic reticulum
 - d. lysosome
-

Solution:

A

Free Response**Exercise:****Problem:**

In the context of cell biology, what do we mean by form follows function? What are at least two examples of this concept?

Solution:

“Form follows function” refers to the idea that the function of a body part dictates the form of that body part. As an example, organisms like birds or fish that fly or swim quickly through the air or water have streamlined bodies that reduce drag. At the level of the cell, in tissues involved in secretory functions, such as the salivary glands, the cells have abundant Golgi.

Glossary**cell wall**

a rigid cell covering made of cellulose in plants, peptidoglycan in bacteria, non-peptidoglycan compounds in Archaea, and chitin in fungi that protects the cell, provides structural support, and gives shape to the cell

central vacuole

a large plant cell organelle that acts as a storage compartment, water reservoir, and site of macromolecule degradation

chloroplast

a plant cell organelle that carries out photosynthesis

cilium

(plural: cilia) a short, hair-like structure that extends from the plasma membrane in large numbers and is used to move an entire cell or move substances along the outer surface of the cell

cytoplasm

the entire region between the plasma membrane and the nuclear envelope, consisting of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals

cytoskeleton

the network of protein fibers that collectively maintains the shape of the cell, secures some organelles in specific positions, allows cytoplasm and vesicles to move within the cell, and enables unicellular organisms to move

cytosol

the gel-like material of the cytoplasm in which cell structures are suspended

desmosome

a linkage between adjacent epithelial cells that forms when cadherins in the plasma membrane attach to intermediate filaments

endomembrane system

the group of organelles and membranes in eukaryotic cells that work together to modify, package, and transport lipids and proteins

endoplasmic reticulum (ER)

a series of interconnected membranous structures within eukaryotic cells that collectively modify proteins and synthesize lipids

extracellular matrix

the material, primarily collagen, glycoproteins, and proteoglycans, secreted from animal cells that holds cells together as a tissue, allows cells to communicate with each other, and provides mechanical protection and anchoring for cells in the tissue

flagellum

(plural: flagella) the long, hair-like structure that extends from the plasma membrane and is used to move the cell

gap junction

a channel between two adjacent animal cells that allows ions, nutrients, and other low-molecular weight substances to pass between the cells, enabling the cells to communicate

Golgi apparatus

a eukaryotic organelle made up of a series of stacked membranes that sorts, tags, and packages lipids and proteins for distribution

lysosome

an organelle in an animal cell that functions as the cell's digestive component; it breaks down proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles

mitochondria

(singular: mitochondrion) the cellular organelles responsible for carrying out cellular respiration, resulting in the production of ATP, the cell's main energy-carrying molecule

nuclear envelope

the double-membrane structure that constitutes the outermost portion of the nucleus

nucleolus

the darkly staining body within the nucleus that is responsible for assembling ribosomal subunits

nucleus

the cell organelle that houses the cell's DNA and directs the synthesis of ribosomes and proteins

peroxisome

a small, round organelle that contains hydrogen peroxide, oxidizes fatty acids and amino acids, and detoxifies many poisons

plasma membrane

a phospholipid bilayer with embedded (integral) or attached (peripheral) proteins that separates the internal contents of the cell from its surrounding environment

plasmodesma

(plural: plasmodesmata) a channel that passes between the cell walls of adjacent plant cells, connects their cytoplasm, and allows materials to be transported from cell to cell

ribosome

a cellular structure that carries out protein synthesis

rough endoplasmic reticulum (RER)

the region of the endoplasmic reticulum that is studded with ribosomes and engages in protein modification

smooth endoplasmic reticulum (SER)

the region of the endoplasmic reticulum that has few or no ribosomes on its cytoplasmic surface and synthesizes carbohydrates, lipids, and steroid hormones; detoxifies chemicals like pesticides, preservatives, medications, and environmental pollutants, and stores calcium ions

tight junction

a firm seal between two adjacent animal cells created by protein adherence

vacuole

a membrane-bound sac, somewhat larger than a vesicle, that functions in cellular storage and transport

vesicle

a small, membrane-bound sac that functions in cellular storage and transport; its membrane is capable of fusing with the plasma membrane and the membranes of the endoplasmic reticulum and Golgi apparatus

The Cell Membrane

By the end of this section, you will be able to:

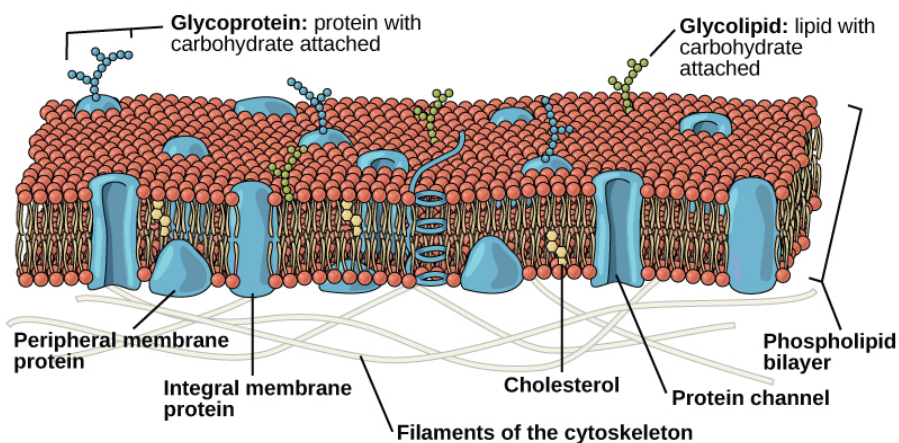
- Understand the fluid mosaic model of membranes
- Describe the functions of phospholipids, proteins, and carbohydrates in membranes

A cell's plasma membrane defines the boundary of the cell and determines the nature of its contact with the environment. Cells exclude some substances, take in others, and excrete still others, all in controlled quantities. Plasma membranes enclose the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux. The plasma membrane must be sufficiently flexible to allow certain cells, such as red blood cells and white blood cells, to change shape as they pass through narrow capillaries. These are the more obvious functions of a plasma membrane. In addition, the surface of the plasma membrane carries markers that allow cells to recognize one another, which is vital as tissues and organs form during early development, and which later plays a role in the “self” versus “non-self” distinction of the immune response.

The plasma membrane also carries receptors, which are attachment sites for specific substances that interact with the cell. Each receptor is structured to bind with a specific substance. For example, surface receptors of the membrane create changes in the interior, such as changes in enzymes of metabolic pathways. These metabolic pathways might be vital for providing the cell with energy, making specific substances for the cell, or breaking down cellular waste or toxins for disposal. Receptors on the plasma membrane's exterior surface interact with hormones or neurotransmitters, and allow their messages to be transmitted into the cell. Some recognition sites are used by viruses as attachment points. Although they are highly specific, pathogens like viruses may evolve to exploit receptors to gain entry to a cell by mimicking the specific substance that the receptor is meant to bind. This specificity helps to explain why human immunodeficiency virus (HIV) or any of the five types of hepatitis viruses invade only specific cells.

Fluid Mosaic Model

In 1972, S. J. Singer and Garth L. Nicolson proposed a new model of the plasma membrane that, compared to earlier understanding, better explained both microscopic observations and the function of the plasma membrane. This was called the **fluid mosaic model**. The model has evolved somewhat over time, but still best accounts for the structure and functions of the plasma membrane as we now understand them. The fluid mosaic model describes the structure of the plasma membrane as a mosaic of components—including phospholipids, cholesterol, proteins, and carbohydrates—in which the components are able to flow and change position, while maintaining the basic integrity of the membrane. Both phospholipid molecules and embedded proteins are able to diffuse rapidly and laterally in the membrane. The fluidity of the plasma membrane is necessary for the activities of certain enzymes and transport molecules within the membrane. Plasma membranes range from 5–10 nm thick. As a comparison, human red blood cells, visible via light microscopy, are approximately 8 μm thick, or approximately 1,000 times thicker than a plasma membrane. ([link](#))



The fluid mosaic model of the plasma membrane structure describes the plasma membrane as a fluid combination of phospholipids, cholesterol, proteins, and carbohydrates.

The plasma membrane is made up primarily of a bilayer of phospholipids with embedded proteins, carbohydrates, glycolipids, and glycoproteins, and, in animal cells, cholesterol. The amount of cholesterol in animal plasma membranes regulates the fluidity of the membrane and changes based on the temperature of the cell's environment. In other words, cholesterol acts as antifreeze in the cell membrane and is more abundant in animals that live in cold climates.

The main fabric of the membrane is composed of two layers of phospholipid molecules, and the polar ends of these molecules (which look like a collection of balls in an artist's rendition of the model) ([\[link\]](#)) are in contact with aqueous fluid both inside and outside the cell. Thus, both surfaces of the plasma membrane are hydrophilic. In contrast, the interior of the membrane, between its two surfaces, is a hydrophobic or nonpolar region because of the fatty acid tails. This region has no attraction for water or other polar molecules.

Proteins make up the second major chemical component of plasma membranes. Integral proteins are embedded in the plasma membrane and may span all or part of the membrane. Integral proteins may serve as channels or pumps to move materials into or out of the cell. Peripheral proteins are found on the exterior or interior surfaces of membranes, attached either to integral proteins or to phospholipid molecules. Both integral and peripheral proteins may serve as enzymes, as structural attachments for the fibers of the cytoskeleton, or as part of the cell's recognition sites.

Carbohydrates are the third major component of plasma membranes. They are always found on the exterior surface of cells and are bound either to proteins (forming glycoproteins) or to lipids (forming glycolipids). These carbohydrate chains may consist of 2–60 monosaccharide units and may be either straight or branched. Along with peripheral proteins, carbohydrates form specialized sites on the cell surface that allow cells to recognize each other.

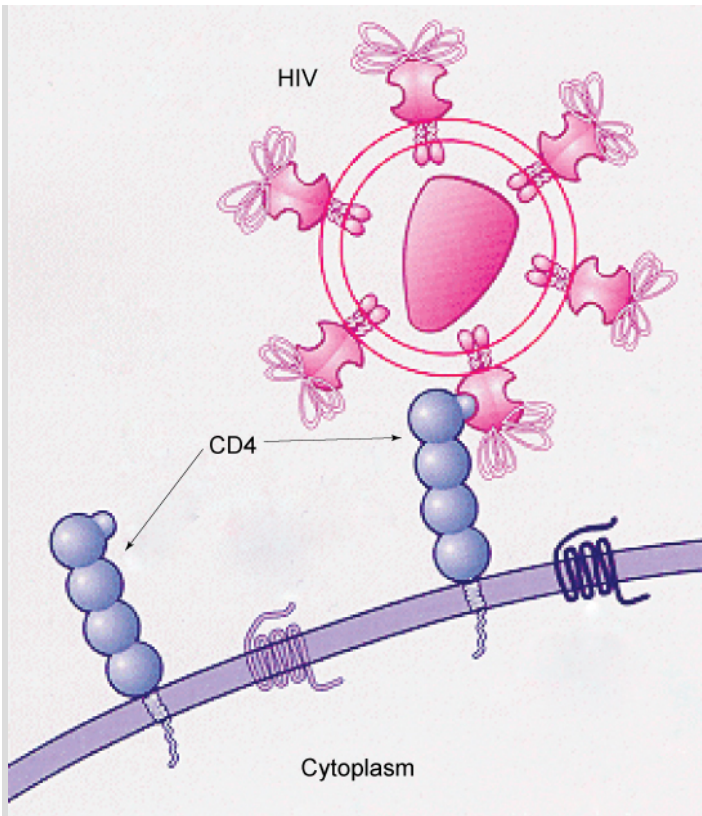
Note:

Evolution in Action

How Viruses Infect Specific Organs

Specific glycoprotein molecules exposed on the surface of the cell membranes of host cells are exploited by many viruses to infect specific organs. For example, HIV is able to penetrate the plasma membranes of specific kinds of white blood cells called T-helper cells and monocytes, as well as some cells of the central nervous system. The hepatitis virus attacks only liver cells.

These viruses are able to invade these cells, because the cells have binding sites on their surfaces that the viruses have exploited with equally specific glycoproteins in their coats. ([link](#)). The cell is tricked by the mimicry of the virus coat molecules, and the virus is able to enter the cell. Other recognition sites on the virus's surface interact with the human immune system, prompting the body to produce antibodies. Antibodies are made in response to the antigens (or proteins associated with invasive pathogens). These same sites serve as places for antibodies to attach, and either destroy or inhibit the activity of the virus. Unfortunately, these sites on HIV are encoded by genes that change quickly, making the production of an effective vaccine against the virus very difficult. The virus population within an infected individual quickly evolves through mutation into different populations, or variants, distinguished by differences in these recognition sites. This rapid change of viral surface markers decreases the effectiveness of the person's immune system in attacking the virus, because the antibodies will not recognize the new variations of the surface patterns.



HIV docks at and binds to the CD4 receptor, a glycoprotein on the surface of T cells, before entering, or infecting, the cell. (credit: modification of work by US National Institutes of Health/National Institute of Allergy and Infectious Diseases)

Section Summary

The modern understanding of the plasma membrane is referred to as the fluid mosaic model. The plasma membrane is composed of a bilayer of phospholipids, with their hydrophobic, fatty acid tails in contact with each other. The landscape of the membrane is studded with proteins, some of

which span the membrane. Some of these proteins serve to transport materials into or out of the cell. Carbohydrates are attached to some of the proteins and lipids on the outward-facing surface of the membrane. These form complexes that function to identify the cell to other cells. The fluid nature of the membrane owes itself to the configuration of the fatty acid tails, the presence of cholesterol embedded in the membrane (in animal cells), and the mosaic nature of the proteins and protein-carbohydrate complexes, which are not firmly fixed in place. Plasma membranes enclose the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux.

Multiple Choice

Exercise:

Problem:

Which plasma membrane component can be either found on its surface or embedded in the membrane structure?

- a. protein
- b. cholesterol
- c. carbohydrate
- d. phospholipid

Solution:

A

Exercise:

Problem:

The tails of the phospholipids of the plasma membrane are composed of _____ and are _____?

- a. phosphate groups; hydrophobic
- b. fatty acid groups; hydrophilic

- c. phosphate groups; hydrophilic
- d. fatty acid groups; hydrophobic

Solution:

D

Free Response

Exercise:

Problem:

Why is it advantageous for the cell membrane to be fluid in nature?

Solution:

The fluidity of the cell membrane is necessary for the operation of some enzymes and transport mechanisms within the membrane.

Glossary

fluid mosaic model

a model of the structure of the plasma membrane as a mosaic of components, including phospholipids, cholesterol, proteins, and glycolipids, resulting in a fluid rather than static character

Introduction

class="introduction"

A hummingbird needs energy to maintain prolonged flight. The bird obtains its energy from taking in food and transforming the energy contained in food molecules into forms of energy to power its flight through a series of biochemical reactions.
(credit: modification of work by Cory Zanker)



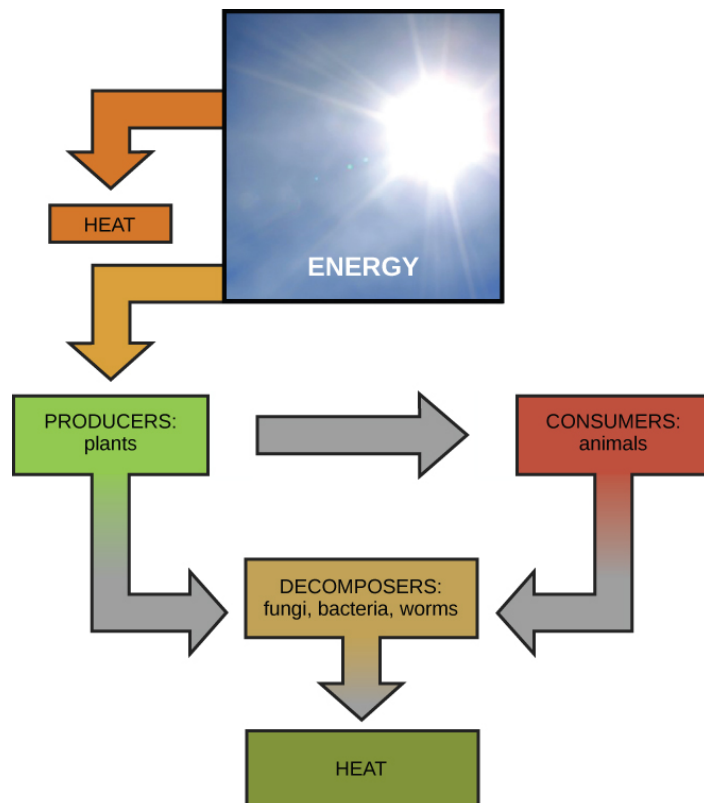
Virtually every task performed by living organisms requires energy. Energy is needed to perform heavy labor and exercise, but humans also use energy while thinking, and even during sleep. In fact, the living cells of every organism constantly use energy. Nutrients and other molecules are imported into the cell, metabolized (broken down) and possibly synthesized into new molecules, modified if needed, transported around the cell, and possibly distributed to the entire organism. For example, the large proteins that make up muscles are built from smaller molecules imported from dietary amino acids. Complex carbohydrates are broken down into simple sugars that the cell uses for energy. Just as energy is required to both build and demolish a building, energy is required for the synthesis and breakdown of molecules as well as the transport of molecules into and out of cells. In addition, processes such as ingesting and breaking down pathogenic bacteria and viruses, exporting wastes and toxins, and movement of the cell require energy. From where, and in what form, does this energy come? How do living cells obtain energy, and how do they use it? This chapter will discuss different forms of energy and the physical laws that govern energy transfer. This chapter will also describe how cells use energy and replenish it, and how chemical reactions in the cell are performed with great efficiency.

Energy and Metabolism

By the end of this section, you will be able to:

- Explain what metabolic pathways are
- State the first and second laws of thermodynamics
- Explain the difference between kinetic and potential energy
- Describe endergonic and exergonic reactions
- Discuss how enzymes function as molecular catalysts

Scientists use the term **bioenergetics** to describe the concept of energy flow ([\[link\]](#)) through living systems, such as cells. Cellular processes such as the building and breaking down of complex molecules occur through stepwise chemical reactions. Some of these chemical reactions are spontaneous and release energy, whereas others require energy to proceed. Just as living things must continually consume food to replenish their energy supplies, cells must continually produce more energy to replenish that used by the many energy-requiring chemical reactions that constantly take place. Together, all of the chemical reactions that take place inside cells, including those that consume or generate energy, are referred to as the cell's **metabolism**.

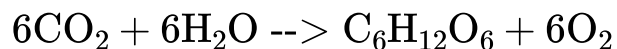


Ultimately, most life forms get their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat the plants to obtain energy. Carnivores eat the herbivores, and eventual decomposition of plant and animal material contributes to the nutrient pool.

Metabolic Pathways

Consider the metabolism of sugar. This is a classic example of one of the many cellular processes that use and produce energy. Living things consume sugars as a major energy source, because sugar molecules have a great deal of energy stored within their bonds. For the most part, photosynthesizing organisms like plants produce these sugars. During photosynthesis, plants use energy (originally from sunlight) to convert carbon dioxide gas (CO₂) into sugar molecules (like glucose: C₆H₁₂O₆). They consume carbon dioxide and produce oxygen as a waste product. This reaction is summarized as:

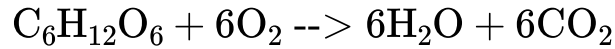
Equation:



Because this process involves synthesizing an energy-storing molecule, it requires energy input to proceed. During the light reactions of photosynthesis, energy is provided by a molecule called adenosine triphosphate (ATP), which is the primary energy currency of all cells. Just as the dollar is used as currency to buy goods, cells use molecules of ATP as energy currency to perform immediate work. In contrast, energy-storage molecules such as glucose are consumed only to be broken down to use their energy. The reaction that harvests the energy of a sugar molecule in cells requiring oxygen to survive can be summarized by the reverse reaction

to photosynthesis. In this reaction, oxygen is consumed and carbon dioxide is released as a waste product. The reaction is summarized as:

Equation:

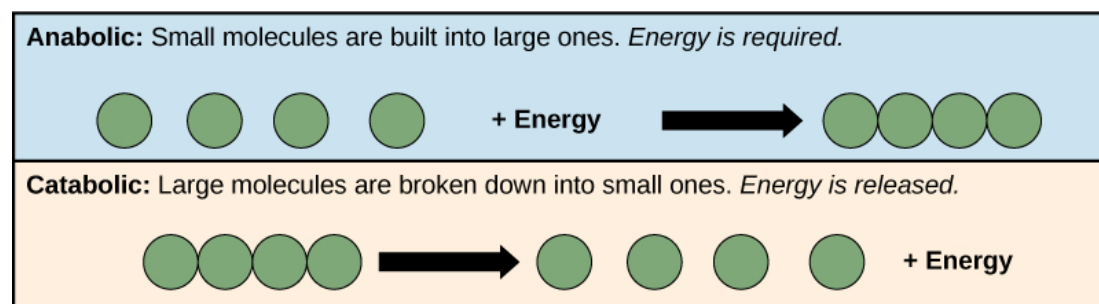


Both of these reactions involve many steps.

The processes of making and breaking down sugar molecules illustrate two examples of metabolic pathways. A metabolic pathway is a series of chemical reactions that takes a starting molecule and modifies it, step-by-step, through a series of metabolic intermediates, eventually yielding a final product. In the example of sugar metabolism, the first metabolic pathway synthesized sugar from smaller molecules, and the other pathway broke sugar down into smaller molecules. These two opposite processes—the first requiring energy and the second producing energy—are referred to as **anabolic** pathways (building polymers) and **catabolic** pathways (breaking down polymers into their monomers), respectively. Consequently, metabolism is composed of synthesis (anabolism) and degradation (catabolism) ([link](#)).

It is important to know that the chemical reactions of metabolic pathways do not take place on their own. Each reaction step is facilitated, or catalyzed, by a protein called an enzyme. Enzymes are important for catalyzing all types of biological reactions—those that require energy as well as those that release energy.

Metabolic pathways



Catabolic pathways are those that generate energy by breaking down larger molecules. Anabolic pathways are those that require energy to synthesize larger molecules. Both types of pathways are required for maintaining the cell's energy balance.

Energy

Thermodynamics refers to the study of energy and energy transfer involving physical matter. The matter relevant to a particular case of energy transfer is called a system, and everything outside of that matter is called the surroundings. For instance, when heating a pot of water on the stove, the system includes the stove, the pot, and the water. Energy is transferred within the system (between the stove, pot, and water). There are two types of systems: open and closed. In an open system, energy can be exchanged with its surroundings. The stovetop system is open because heat can be lost to the air. A closed system cannot exchange energy with its surroundings.

Biological organisms are open systems. Energy is exchanged between them and their surroundings as they use energy from the sun to perform photosynthesis or consume energy-storing molecules and release energy to the environment by doing work and releasing heat. Like all things in the physical world, energy is subject to physical laws. The laws of thermodynamics govern the transfer of energy in and among all systems in the universe.

In general, energy is defined as the ability to do work, or to create some kind of change. Energy exists in different forms. For example, electrical energy, light energy, and heat energy are all different types of energy. To appreciate the way energy flows into and out of biological systems, it is important to understand two of the physical laws that govern energy.

Thermodynamics

The first law of thermodynamics states that the total amount of energy in the universe is constant and conserved. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transferred from place to place or transformed into different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. Light bulbs transform electrical energy into light and heat energy. Gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful energy transformations on earth: that of converting the energy of sunlight to chemical energy stored within organic molecules ([\[link\]](#)). Some examples of energy transformations are shown in [\[link\]](#).

The challenge for all living organisms is to obtain energy from their surroundings in forms that they can transfer or transform into usable energy to do work. Living cells have evolved to meet this challenge. Chemical energy stored within organic molecules such as sugars and fats is transferred and transformed through a series of cellular chemical reactions into energy within molecules of ATP. Energy in ATP molecules is easily accessible to do work. Examples of the types of work that cells need to do include building complex molecules, transporting materials, powering the motion of cilia or flagella, and contracting muscle fibers to create movement.

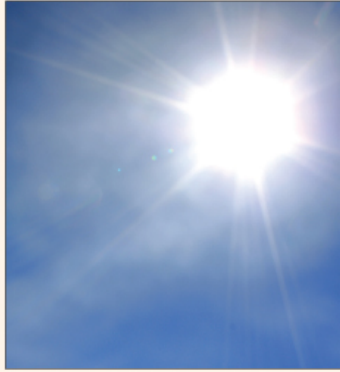
Energy Transformations



Chemical energy



Kinetic energy



Light energy



Chemical energy



Shown are some examples of energy transferred and transformed from one system to another and from one form to another. The food we consume provides our cells with the energy required to carry out bodily functions, just as light energy provides plants with the means to create the chemical energy they need. (credit "ice cream": modification of work by D. Sharon Pruitt; credit "kids": modification of work by Max from Providence; credit "leaf": modification of work by Cory Zanker)

A living cell's primary tasks of obtaining, transforming, and using energy to do work may seem simple. However, the second law of thermodynamics explains why these tasks are harder than they appear. All energy transfers and transformations are never completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this form is heat energy. Thermodynamically, **heat energy** is defined as the energy transferred from one system to another that is not work. For example, when a light bulb is turned on, some of the energy being converted from electrical energy into light energy is lost as heat energy. Likewise, some energy is lost as heat energy during cellular metabolic reactions.

An important concept in physical systems is that of order and disorder. The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists refer to the measure of randomness or disorder within a system as entropy. High entropy means high disorder and low energy. Molecules and chemical reactions have varying entropy as well. For example, entropy increases as molecules at a high concentration in one place diffuse and spread out. The second law of thermodynamics says that energy will always be lost as heat in energy transfers or transformations.

Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy.

Potential and Kinetic Energy

When an object is in motion, there is energy associated with that object. Think of a wrecking ball. Even a slow-moving wrecking ball can do a great deal of damage to other objects. Energy associated with objects in motion is called **kinetic energy** ([\[link\]](#)). A speeding bullet, a walking person, and the rapid movement of molecules in the air (which produces heat) all have kinetic energy.

Now what if that same motionless wrecking ball is lifted two stories above ground with a crane? If the suspended wrecking ball is unmoving, is there

energy associated with it? The answer is yes. The energy that was required to lift the wrecking ball did not disappear, but is now stored in the wrecking ball by virtue of its position and the force of gravity acting on it. This type of energy is called **potential energy** ([link](#)). If the ball were to fall, the potential energy would be transformed into kinetic energy until all of the potential energy was exhausted when the ball rested on the ground. Wrecking balls also swing like a pendulum; through the swing, there is a constant change of potential energy (highest at the top of the swing) to kinetic energy (highest at the bottom of the swing). Other examples of potential energy include the energy of water held behind a dam or a person about to skydive out of an airplane.



Still water has potential energy; moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy.
(credit "dam": modification of work by "Pascal"/Flickr;
credit "waterfall": modification of work by Frank Gualtieri)

Potential energy is not only associated with the location of matter, but also with the structure of matter. Even a spring on the ground has potential energy if it is compressed; so does a rubber band that is pulled taut. On a molecular level, the bonds that hold the atoms of molecules together exist in a particular structure that has potential energy. Remember that anabolic

cellular pathways require energy to synthesize complex molecules from simpler ones and catabolic pathways release energy when complex molecules are broken down. The fact that energy can be released by the breakdown of certain chemical bonds implies that those bonds have potential energy. In fact, there is potential energy stored within the bonds of all the food molecules we eat, which is eventually harnessed for use. This is because these bonds can release energy when broken. The type of potential energy that exists within chemical bonds, and is released when those bonds are broken, is called chemical energy. Chemical energy is responsible for providing living cells with energy from food. The release of energy occurs when the molecular bonds within food molecules are broken.

Note:**Concept in Action**

Visit the [site](#) and select “Pendulum” from the “Work and Energy” menu to see the shifting kinetic and potential energy of a pendulum in motion.

Free and Activation Energy

After learning that chemical reactions release energy when energy-storing bonds are broken, an important next question is the following: How is the energy associated with these chemical reactions quantified and expressed? How can the energy released from one reaction be compared to that of another reaction? A measurement of free energy is used to quantify these energy transfers. Recall that according to the second law of thermodynamics, all energy transfers involve the loss of some amount of energy in an unusable form such as heat. Free energy specifically refers to

the energy associated with a chemical reaction that is available after the losses are accounted for. In other words, free energy is usable energy, or energy that is available to do work.

If energy is released during a chemical reaction, then the change in free energy, signified as ΔG (delta G) will be a negative number. A negative change in free energy also means that the products of the reaction have less free energy than the reactants, because they release some free energy during the reaction. Reactions that have a negative change in free energy and consequently release free energy are called **exergonic reactions**. Think: exergonic means energy is exiting the system. These reactions are also referred to as spontaneous reactions, and their products have less stored energy than the reactants. An important distinction must be drawn between the term spontaneous and the idea of a chemical reaction occurring immediately. Contrary to the everyday use of the term, a spontaneous reaction is not one that suddenly or quickly occurs. The rusting of iron is an example of a spontaneous reaction that occurs slowly, little by little, over time.

If a chemical reaction absorbs energy rather than releases energy on balance, then the ΔG for that reaction will be a positive value. In this case, the products have more free energy than the reactants. Thus, the products of these reactions can be thought of as energy-storing molecules. These chemical reactions are called **endergonic reactions** and they are non-spontaneous. An endergonic reaction will not take place on its own without the addition of free energy.

Note:

Art Connection



(a)



(b)



(c)



(d)

Shown are some examples of endergonic processes (ones that require energy) and exergonic processes (ones that release energy). (credit a: modification of work by Natalie Maynor; credit b: modification of work by USDA; credit c: modification of work by Cory Zanker; credit d: modification of work by Harry Malsch)

Look at each of the processes shown and decide if it is endergonic or exergonic.

There is another important concept that must be considered regarding endergonic and exergonic reactions. Exergonic reactions require a small amount of energy input to get going, before they can proceed with their

energy-releasing steps. These reactions have a net release of energy, but still require some energy input in the beginning. This small amount of energy input necessary for all chemical reactions to occur is called the **activation energy**.

Note:

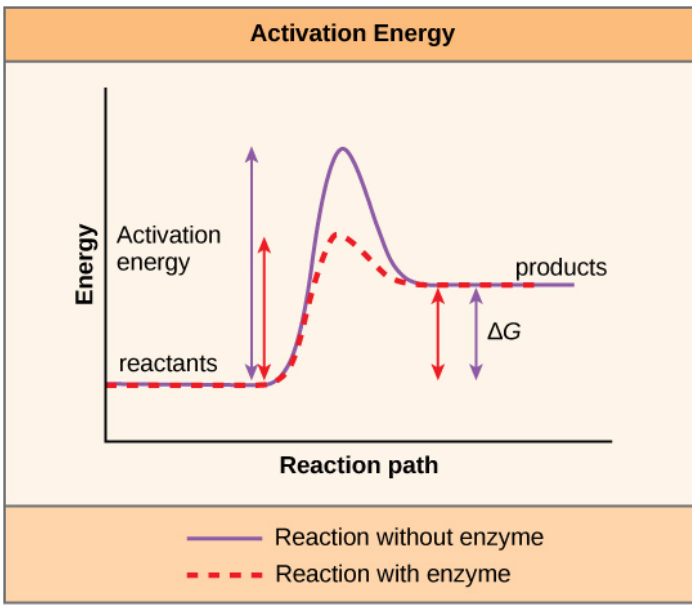
Concept in Action



Watch an [animation](#) of the move from free energy to transition state of the reaction.

Enzymes

A substance that helps a chemical reaction to occur is called a catalyst, and the molecules that catalyze biochemical reactions are called **enzymes**. Most enzymes are proteins and perform the critical task of lowering the activation energies of chemical reactions inside the cell. Most of the reactions critical to a living cell happen too slowly at normal temperatures to be of any use to the cell. Without enzymes to speed up these reactions, life could not persist. Enzymes do this by binding to the reactant molecules and holding them in such a way as to make the chemical bond-breaking and -forming processes take place more easily. It is important to remember that enzymes do not change whether a reaction is exergonic (spontaneous) or endergonic. This is because they do not change the free energy of the reactants or products. They only reduce the activation energy required for the reaction to go forward ([\[link\]](#)). In addition, an enzyme itself is unchanged by the reaction it catalyzes. Once one reaction has been catalyzed, the enzyme is able to participate in other reactions.



Enzymes lower the activation energy of the reaction but do not change the free energy of the reaction.

The chemical reactants to which an enzyme binds are called the enzyme's **substrates**. There may be one or more substrates, depending on the particular chemical reaction. In some reactions, a single reactant substrate is broken down into multiple products. In others, two substrates may come together to create one larger molecule. Two reactants might also enter a reaction and both become modified, but they leave the reaction as two products. The location within the enzyme where the substrate binds is called the enzyme's **active site**. The active site is where the “action” happens. Since enzymes are proteins, there is a unique combination of amino acid side chains within the active site. Each side chain is characterized by different properties. They can be large or small, weakly acidic or basic, hydrophilic or hydrophobic, positively or negatively charged, or neutral. The unique combination of side chains creates a very specific chemical environment within the active site. This specific environment is suited to bind to one specific chemical substrate (or substrates).

Active sites are subject to influences of the local environment. Increasing the environmental temperature generally increases reaction rates, enzyme-catalyzed or otherwise. However, temperatures outside of an optimal range reduce the rate at which an enzyme catalyzes a reaction. Hot temperatures will eventually cause enzymes to denature, an irreversible change in the three-dimensional shape and therefore the function of the enzyme. Enzymes are also suited to function best within a certain pH and salt concentration range, and, as with temperature, extreme pH, and salt concentrations can cause enzymes to denature.

For many years, scientists thought that enzyme-substrate binding took place in a simple “lock and key” fashion. This model asserted that the enzyme and substrate fit together perfectly in one instantaneous step. However, current research supports a model called induced fit ([\[link\]](#)). The induced-fit model expands on the lock-and-key model by describing a more dynamic binding between enzyme and substrate. As the enzyme and substrate come together, their interaction causes a mild shift in the enzyme’s structure that forms an ideal binding arrangement between enzyme and substrate.

Note:

Concept in Action

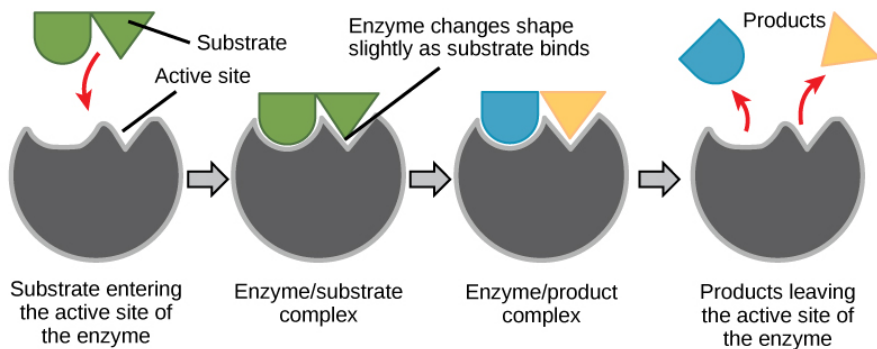


View an [animation](#) of induced fit.

When an enzyme binds its substrate, an enzyme-substrate complex is formed. This complex lowers the activation energy of the reaction and promotes its rapid progression in one of multiple possible ways. On a basic level, enzymes promote chemical reactions that involve more than one

substrate by bringing the substrates together in an optimal orientation for reaction. Another way in which enzymes promote the reaction of their substrates is by creating an optimal environment within the active site for the reaction to occur. The chemical properties that emerge from the particular arrangement of amino acid R groups within an active site create the perfect environment for an enzyme's specific substrates to react.

The enzyme-substrate complex can also lower activation energy by compromising the bond structure so that it is easier to break. Finally, enzymes can also lower activation energies by taking part in the chemical reaction itself. In these cases, it is important to remember that the enzyme will always return to its original state by the completion of the reaction. One of the hallmark properties of enzymes is that they remain ultimately unchanged by the reactions they catalyze. After an enzyme has catalyzed a reaction, it releases its product(s) and can catalyze a new reaction.



The induced-fit model is an adjustment to the lock-and-key model and explains how enzymes and substrates undergo dynamic modifications during the transition state to increase the affinity of the substrate for the active site.

It would seem ideal to have a scenario in which all of an organism's enzymes existed in abundant supply and functioned optimally under all cellular conditions, in all cells, at all times. However, a variety of

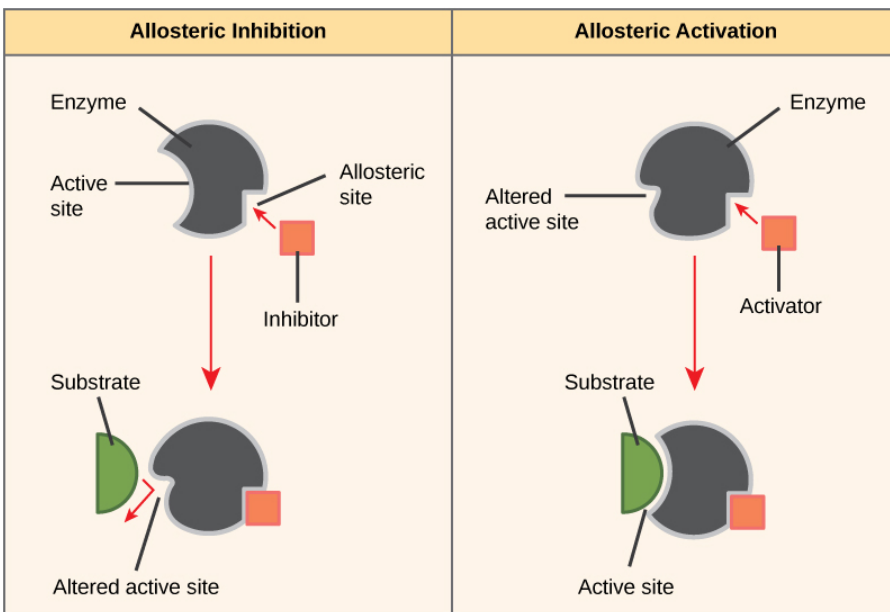
mechanisms ensures that this does not happen. Cellular needs and conditions constantly vary from cell to cell, and change within individual cells over time. The required enzymes of stomach cells differ from those of fat storage cells, skin cells, blood cells, and nerve cells. Furthermore, a digestive organ cell works much harder to process and break down nutrients during the time that closely follows a meal compared with many hours after a meal. As these cellular demands and conditions vary, so must the amounts and functionality of different enzymes.

Since the rates of biochemical reactions are controlled by activation energy, and enzymes lower and determine activation energies for chemical reactions, the relative amounts and functioning of the variety of enzymes within a cell ultimately determine which reactions will proceed and at what rates. This determination is tightly controlled in cells. In certain cellular environments, enzyme activity is partly controlled by environmental factors like pH, temperature, salt concentration, and, in some cases, cofactors or coenzymes.

Enzymes can also be regulated in ways that either promote or reduce enzyme activity. There are many kinds of molecules that inhibit or promote enzyme function, and various mechanisms by which they do so. In some cases of enzyme inhibition, an inhibitor molecule is similar enough to a substrate that it can bind to the active site and simply block the substrate from binding. When this happens, the enzyme is inhibited through **competitive inhibition**, because an inhibitor molecule competes with the substrate for binding to the active site.

On the other hand, in **noncompetitive inhibition**, an inhibitor molecule binds to the enzyme in a location other than the active site, called an allosteric site, but still manages to block substrate binding to the active site. Some inhibitor molecules bind to enzymes in a location where their binding induces a conformational change that reduces the affinity of the enzyme for its substrate. This type of inhibition is called **allosteric inhibition** ([\[link\]](#)). Most allosterically regulated enzymes are made up of more than one polypeptide, meaning that they have more than one protein subunit. When an allosteric inhibitor binds to a region on an enzyme, all active sites on the protein subunits are changed slightly such that they bind their substrates

with less efficiency. There are allosteric activators as well as inhibitors. Allosteric activators bind to locations on an enzyme away from the active site, inducing a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s) ([link](#)).



Allosteric inhibition works by indirectly inducing a conformational change to the active site such that the substrate no longer fits. In contrast, in allosteric activation, the activator molecule modifies the shape of the active site to allow a better fit of the substrate.

Note:

Careers in Action

Pharmaceutical Drug Developer



Have you ever wondered
how pharmaceutical
drugs are developed?
(credit: Deborah Austin)

Enzymes are key components of metabolic pathways. Understanding how enzymes work and how they can be regulated are key principles behind the development of many of the pharmaceutical drugs on the market today. Biologists working in this field collaborate with other scientists to design drugs ([\[link\]](#)).

Consider statins for example—statins is the name given to one class of drugs that can reduce cholesterol levels. These compounds are inhibitors of the enzyme HMG-CoA reductase, which is the enzyme that synthesizes cholesterol from lipids in the body. By inhibiting this enzyme, the level of cholesterol synthesized in the body can be reduced. Similarly, acetaminophen, popularly marketed under the brand name Tylenol, is an inhibitor of the enzyme cyclooxygenase. While it is used to provide relief from fever and inflammation (pain), its mechanism of action is still not completely understood.

How are drugs discovered? One of the biggest challenges in drug discovery is identifying a drug target. A drug target is a molecule that is literally the target of the drug. In the case of statins, HMG-CoA reductase is the drug target. Drug targets are identified through painstaking research in the laboratory. Identifying the target alone is not enough; scientists also need to know how the target acts inside the cell and which reactions go awry in the case of disease. Once the target and the pathway are identified, then the actual process of drug design begins. In this stage, chemists and

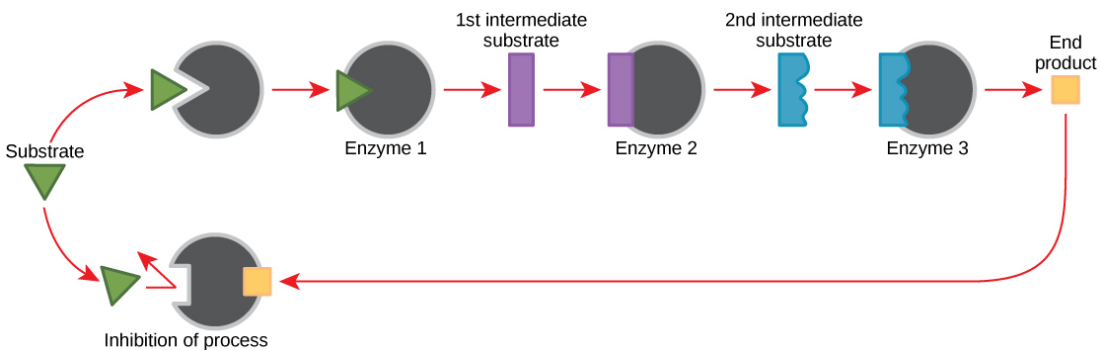
biologists work together to design and synthesize molecules that can block or activate a particular reaction. However, this is only the beginning: If and when a drug prototype is successful in performing its function, then it is subjected to many tests from in vitro experiments to clinical trials before it can get approval from the U.S. Food and Drug Administration to be on the market.

Many enzymes do not work optimally, or even at all, unless bound to other specific non-protein helper molecules. They may bond either temporarily through ionic or hydrogen bonds, or permanently through stronger covalent bonds. Binding to these molecules promotes optimal shape and function of their respective enzymes. Two examples of these types of helper molecules are cofactors and coenzymes. Cofactors are inorganic ions such as ions of iron and magnesium. Coenzymes are organic helper molecules, those with a basic atomic structure made up of carbon and hydrogen. Like enzymes, these molecules participate in reactions without being changed themselves and are ultimately recycled and reused. Vitamins are the source of coenzymes. Some vitamins are the precursors of coenzymes and others act directly as coenzymes. Vitamin C is a direct coenzyme for multiple enzymes that take part in building the important connective tissue, collagen. Therefore, enzyme function is, in part, regulated by the abundance of various cofactors and coenzymes, which may be supplied by an organism's diet or, in some cases, produced by the organism.

Feedback Inhibition in Metabolic Pathways

Molecules can regulate enzyme function in many ways. The major question remains, however: What are these molecules and where do they come from? Some are cofactors and coenzymes, as you have learned. What other molecules in the cell provide enzymatic regulation such as allosteric modulation, and competitive and non-competitive inhibition? Perhaps the most relevant sources of regulatory molecules, with respect to enzymatic cellular metabolism, are the products of the cellular metabolic reactions themselves. In a most efficient and elegant way, cells have evolved to use

the products of their own reactions for feedback inhibition of enzyme activity. **Feedback inhibition** involves the use of a reaction product to regulate its own further production ([\[link\]](#)). The cell responds to an abundance of the products by slowing down production during anabolic or catabolic reactions. Such reaction products may inhibit the enzymes that catalyzed their production through the mechanisms described above.



Metabolic pathways are a series of reactions catalyzed by multiple enzymes. Feedback inhibition, where the end product of the pathway inhibits an upstream process, is an important regulatory mechanism in cells.

The production of both amino acids and nucleotides is controlled through feedback inhibition. Additionally, ATP is an allosteric regulator of some of the enzymes involved in the catabolic breakdown of sugar, the process that creates ATP. In this way, when ATP is in abundant supply, the cell can prevent the production of ATP. On the other hand, ADP serves as a positive allosteric regulator (an allosteric activator) for some of the same enzymes that are inhibited by ATP. Thus, when relative levels of ADP are high compared to ATP, the cell is triggered to produce more ATP through sugar catabolism.

Section Summary

Cells perform the functions of life through various chemical reactions. A cell's metabolism refers to the combination of chemical reactions that take place within it. Catabolic reactions break down complex chemicals into simpler ones and are associated with energy release. Anabolic processes build complex molecules out of simpler ones and require energy.

In studying energy, the term system refers to the matter and environment involved in energy transfers. Entropy is a measure of the disorder of a system. The physical laws that describe the transfer of energy are the laws of thermodynamics. The first law states that the total amount of energy in the universe is constant. The second law of thermodynamics states that every energy transfer involves some loss of energy in an unusable form, such as heat energy. Energy comes in different forms: kinetic, potential, and free. The change in free energy of a reaction can be negative (releases energy, exergonic) or positive (consumes energy, endergonic). All reactions require an initial input of energy to proceed, called the activation energy.

Enzymes are chemical catalysts that speed up chemical reactions by lowering their activation energy. Enzymes have an active site with a unique chemical environment that fits particular chemical reactants for that enzyme, called substrates. Enzymes and substrates are thought to bind according to an induced-fit model. Enzyme action is regulated to conserve resources and respond optimally to the environment.

Art Connections

Exercise:

Problem:

[\[link\]](#) Look at each of the processes shown and decide if it is endergonic or exergonic.

Solution:

[\[link\]](#) A compost pile decomposing is an exergonic process. A baby developing from a fertilized egg is an endergonic process. Tea

dissolving into water is an exergonic process. A ball rolling downhill is an exergonic process.

Review Questions

Exercise:

Problem:

Which of the following is not an example of an energy transformation?

- a. Heating up dinner in a microwave
- b. Solar panels at work
- c. Formation of static electricity
- d. None of the above

Solution:

D

Exercise:

Problem: Which of the following is not true about enzymes?

- a. They are consumed by the reactions they catalyze.
- b. They are usually made of amino acids.
- c. They lower the activation energy of chemical reactions.
- d. Each one is specific to the particular substrate(s) to which it binds.

Solution:

A

Free Response

Exercise:**Problem:**

Does physical exercise to increase muscle mass involve anabolic and/or catabolic processes? Give evidence for your answer.

Solution:

Physical exercise involves both anabolic and catabolic processes. Body cells break down sugars to provide ATP to do the work necessary for exercise, such as muscle contractions. This is catabolism. Muscle cells also must repair muscle tissue damaged by exercise by building new muscle. This is anabolism.

Exercise:**Problem:**

Explain in your own terms the difference between a spontaneous reaction and one that occurs instantaneously, and what causes this difference.

Solution:

A spontaneous reaction is one that has a negative ΔG and thus releases energy. However, a spontaneous reaction need not occur quickly or suddenly like an instantaneous reaction. It may occur over long periods of time due to a large energy of activation, which prevents the reaction from occurring quickly.

Exercise:**Problem:**

With regard to enzymes, why are vitamins and minerals necessary for good health? Give examples.

Solution:

Most vitamins and minerals act as cofactors and coenzymes for enzyme action. Many enzymes require the binding of certain cofactors or coenzymes to be able to catalyze their reactions. Since enzymes catalyze many important reactions, it is critical to obtain sufficient vitamins and minerals from diet and supplements. Vitamin C (ascorbic acid) is a coenzyme necessary for the action of enzymes that build collagen.

Glossary

activation energy

the amount of initial energy necessary for reactions to occur

active site

a specific region on the enzyme where the substrate binds

allosteric inhibition

the mechanism for inhibiting enzyme action in which a regulatory molecule binds to a second site (not the active site) and initiates a conformation change in the active site, preventing binding with the substrate

anabolic

describes the pathway that requires a net energy input to synthesize complex molecules from simpler ones

bioenergetics

the concept of energy flow through living systems

catabolic

describes the pathway in which complex molecules are broken down into simpler ones, yielding energy as an additional product of the reaction

competitive inhibition

a general mechanism of enzyme activity regulation in which a molecule other than the enzyme's substrate is able to bind the active

site and prevent the substrate itself from binding, thus inhibiting the overall rate of reaction for the enzyme

endergonic

describes a chemical reaction that results in products that store more chemical potential energy than the reactants

enzyme

a molecule that catalyzes a biochemical reaction

exergonic

describes a chemical reaction that results in products with less chemical potential energy than the reactants, plus the release of free energy

feedback inhibition

a mechanism of enzyme activity regulation in which the product of a reaction or the final product of a series of sequential reactions inhibits an enzyme for an earlier step in the reaction series

heat energy

the energy transferred from one system to another that is not work

kinetic energy

the type of energy associated with objects in motion

metabolism

all the chemical reactions that take place inside cells, including those that use energy and those that release energy

noncompetitive inhibition

a general mechanism of enzyme activity regulation in which a regulatory molecule binds to a site other than the active site and prevents the active site from binding the substrate; thus, the inhibitor molecule does not compete with the substrate for the active site; allosteric inhibition is a form of noncompetitive inhibition

potential energy

the type of energy that refers to the potential to do work

substrate

a molecule on which the enzyme acts

thermodynamics

the science of the relationships between heat, energy, and work

Introduction

class="introduction"

This sage
thrasher's diet,
like that of
almost all
organisms,
depends on
photosynthesis
. (credit:
modification
of work by
Dave Menke,
U.S. Fish and
Wildlife
Service)



No matter how complex or advanced a machine, such as the latest cellular phone, the device cannot function without energy. Living things, similar to machines, have many complex components; they too cannot do anything without energy, which is why humans and all other organisms must “eat” in

some form or another. That may be common knowledge, but how many people realize that every bite of every meal ingested depends on the process of photosynthesis?

Overview of Photosynthesis

By the end of this section, you will be able to:

- Summarize the process of photosynthesis
- Explain the relevance of photosynthesis to other living things
- Identify the reactants and products of photosynthesis
- Describe the main structures involved in photosynthesis

All living organisms on earth consist of one or more cells. Each cell runs on the chemical energy found mainly in carbohydrate molecules (food), and the majority of these molecules are produced by one process: photosynthesis. Through photosynthesis, certain organisms convert solar energy (sunlight) into chemical energy, which is then used to build carbohydrate molecules. The energy used to hold these molecules together is released when an organism breaks down food. Cells then use this energy to perform work, such as cellular respiration.

The energy that is harnessed from photosynthesis enters the ecosystems of our planet continuously and is transferred from one organism to another. Therefore, directly or indirectly, the process of photosynthesis provides most of the energy required by living things on earth.

Photosynthesis also results in the release of oxygen into the atmosphere. In short, to eat and breathe, humans depend almost entirely on the organisms that carry out photosynthesis.

Note:

Concept in Action



Click the following [link](#) to learn more about photosynthesis.

Solar Dependence and Food Production

Some organisms can carry out photosynthesis, whereas others cannot. An **autotroph** is an organism that can produce its own food. The Greek roots of the word *autotroph* mean “self” (*auto*) “feeder” (*troph*). Plants are the best-known autotrophs, but others exist, including certain types of bacteria and algae ([link](#)). Oceanic algae contribute enormous quantities of food and oxygen to global food chains. Plants are also **photoautotrophs**, a type of autotroph that uses sunlight and carbon from carbon dioxide to synthesize chemical energy in the form of carbohydrates. All organisms carrying out photosynthesis require sunlight.



(a) Plants, (b) algae, and (c) certain bacteria, called cyanobacteria, are photoautotrophs that can carry out photosynthesis. Algae can grow over enormous areas in water, at times completely covering the surface. (credit a: Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: "eutrophication&hypoxia"/Flickr; credit c: NASA; scale-bar data from Matt Russell)

Heterotrophs are organisms incapable of photosynthesis that must therefore obtain energy and carbon from food by consuming other organisms. The Greek roots of the word *heterotroph* mean “other” (*hetero*)

“feeder” (*troph*), meaning that their food comes from other organisms. Even if the food organism is another animal, this food traces its origins back to autotrophs and the process of photosynthesis. Humans are heterotrophs, as are all animals. Heterotrophs depend on autotrophs, either directly or indirectly. Deer and wolves are heterotrophs. A deer obtains energy by eating plants. A wolf eating a deer obtains energy that originally came from the plants eaten by that deer. The energy in the plant came from photosynthesis, and therefore it is the only autotroph in this example ([link](#)). Using this reasoning, all food eaten by humans also links back to autotrophs that carry out photosynthesis.



The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer is getting energy that originated in the photosynthetic vegetation that the deer consumed.
(credit: Steve VanRiper, U.S. Fish and Wildlife Service)

Note:

Biology in Action

Photosynthesis at the Grocery Store

Photosynthesis is the origin of the products that comprise the main elements of the human diet. (credit:

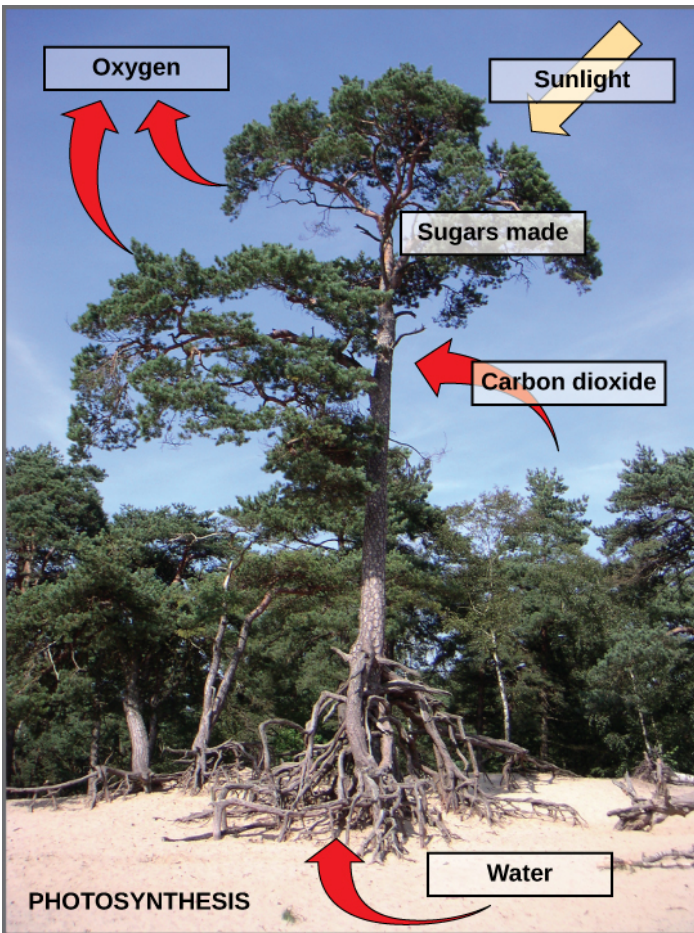
Associação Brasileira de Supermercados)

Major grocery stores in the United States are organized into departments, such as dairy, meats, produce, bread, cereals, and so forth. Each aisle contains hundreds, if not thousands, of different products for customers to buy and consume ([link](#)).

Although there is a large variety, each item links back to photosynthesis. Meats and dairy products link to photosynthesis because the animals were fed plant-based foods. The breads, cereals, and pastas come largely from grains, which are the seeds of photosynthetic plants. What about desserts and drinks? All of these products contain sugar—the basic carbohydrate molecule produced directly from photosynthesis. The photosynthesis connection applies to every meal and every food a person consumes.

Main Structures and Summary of Photosynthesis

Photosynthesis requires sunlight, carbon dioxide, and water as starting reactants ([\[link\]](#)). After the process is complete, photosynthesis releases oxygen and produces carbohydrate molecules, most commonly glucose. These sugar molecules contain the energy that living things need to survive.



Photosynthesis uses solar energy, carbon dioxide, and water to release oxygen and to produce energy-storing sugar molecules.

The complex reactions of photosynthesis can be summarized by the chemical equation shown in [\[link\]](#).

Photosynthesis Equation				
Carbon dioxide	+	Water		Sugar + Oxygen
6CO_2		$6\text{H}_2\text{O}$		$\text{C}_6\text{H}_{12}\text{O}_6$ + 6O_2

The process of photosynthesis can be represented by an equation, wherein carbon dioxide and water produce sugar and oxygen using energy from sunlight.

Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex, as in the way that the reaction summarizing cellular respiration represented many individual reactions. Before learning the details of how photoautotrophs turn sunlight into food, it is important to become familiar with the physical structures involved.

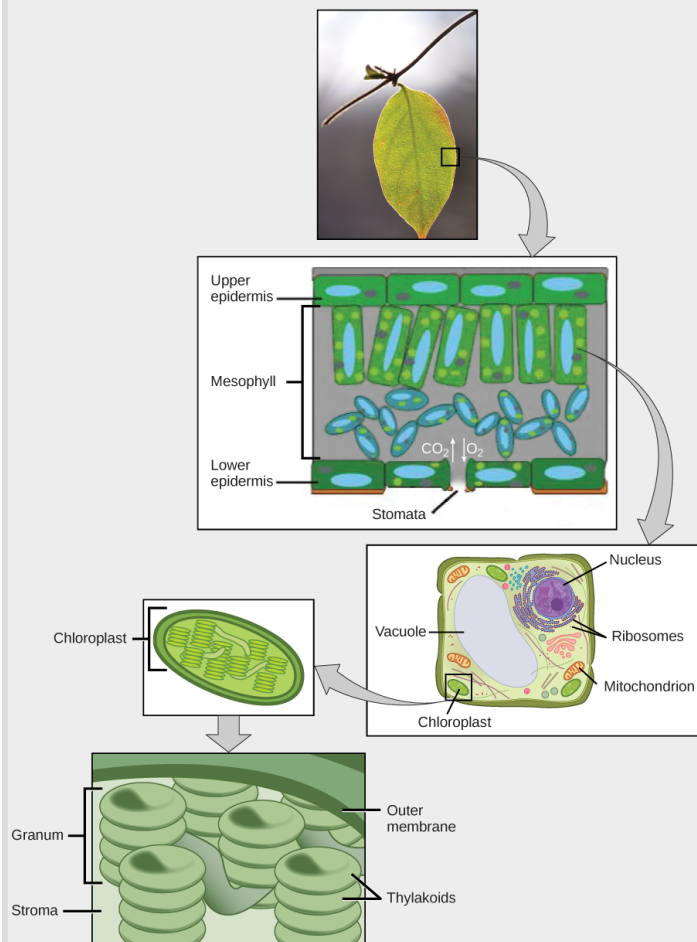
In plants, photosynthesis takes place primarily in leaves, which consist of many layers of cells and have differentiated top and bottom sides. The process of photosynthesis occurs not on the surface layers of the leaf, but rather in a middle layer called the **mesophyll** ([\[link\]](#)). The gas exchange of carbon dioxide and oxygen occurs through small, regulated openings called **stomata**.

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a **chloroplast**. In plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double (inner and outer) membrane. Within the chloroplast is a third membrane that forms stacked, disc-shaped structures called **thylakoids**. Embedded in the thylakoid membrane are molecules of **chlorophyll**, a **pigment** (a molecule that absorbs light) through which the entire process of photosynthesis begins. Chlorophyll is responsible for the green color of plants. The thylakoid membrane encloses an internal space called the thylakoid space. Other types of pigments are also involved in photosynthesis, but chlorophyll is by far the most important. As shown in [\[link\]](#), a stack of thylakoids is called a **granum**, and

the space surrounding the granum is called **stroma** (not to be confused with stomata, the openings on the leaves).

Note:

Art Connection



Not all cells of a leaf carry out photosynthesis. Cells within the middle layer of a leaf have chloroplasts, which contain the photosynthetic apparatus. (credit "leaf": modification of work by Cory Zanker)

On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?

The Two Parts of Photosynthesis

Photosynthesis takes place in two stages: the light-dependent reactions and the Calvin cycle. In the **light-dependent reactions**, which take place at the thylakoid membrane, chlorophyll absorbs energy from sunlight and then converts it into chemical energy with the use of water. The light-dependent reactions release oxygen from the hydrolysis of water as a byproduct. In the Calvin cycle, which takes place in the stroma, the chemical energy derived from the light-dependent reactions drives both the capture of carbon in carbon dioxide molecules and the subsequent assembly of sugar molecules. The two reactions use carrier molecules to transport the energy from one to the other. The carriers that move energy from the light-dependent reactions to the Calvin cycle reactions can be thought of as “full” because they bring energy. After the energy is released, the “empty” energy carriers return to the light-dependent reactions to obtain more energy.

Section Summary

The process of photosynthesis transformed life on earth. By harnessing energy from the sun, photosynthesis allowed living things to access enormous amounts of energy. Because of photosynthesis, living things gained access to sufficient energy, allowing them to evolve new structures and achieve the biodiversity that is evident today.

Only certain organisms, called autotrophs, can perform photosynthesis; they require the presence of chlorophyll, a specialized pigment that can absorb light and convert light energy into chemical energy. Photosynthesis uses carbon dioxide and water to assemble carbohydrate molecules (usually glucose) and releases oxygen into the air. Eukaryotic autotrophs, such as plants and algae, have organelles called chloroplasts in which photosynthesis takes place.

Art Connections

Exercise:

Problem:

[\[link\]](#) On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?

Solution:

[\[link\]](#) Levels of carbon dioxide (a reactant) will fall, and levels of oxygen (a product) will rise. As a result, the rate of photosynthesis will slow down.

Multiple Choice

Exercise:

Problem: What two products result from photosynthesis?

- a. water and carbon dioxide
 - b. water and oxygen
 - c. glucose and oxygen
 - d. glucose and carbon dioxide
-

Solution:

C

Exercise:

Problem:

Which statement about thylakoids in eukaryotes is *not* correct?

- a. Thylakoids are assembled into stacks.
- b. Thylakoids exist as a maze of folded membranes.

- c. The space surrounding thylakoids is called stroma.
- d. Thylakoids contain chlorophyll.

Solution:

B

Exercise:

Problem: From where does a heterotroph directly obtain its energy?

- a. the sun
- b. the sun and eating other organisms
- c. eating other organisms
- d. simple chemicals in the environment

Solution:

C

Free Response

Exercise:

Problem:

What is the overall purpose of the light reactions in photosynthesis?

Solution:

To convert solar energy into chemical energy that cells can use to do work.

Exercise:

Problem:

Why are carnivores, such as lions, dependent on photosynthesis to survive?

Solution:

Because lions eat animals that eat plants.

Glossary

autotroph

an organism capable of producing its own food

chlorophyll

the green pigment that captures the light energy that drives the reactions of photosynthesis

chloroplast

the organelle where photosynthesis takes place

granum

a stack of thylakoids located inside a chloroplast

heterotroph

an organism that consumes other organisms for food

light-dependent reaction

the first stage of photosynthesis where visible light is absorbed to form two energy-carrying molecules (ATP and NADPH)

mesophyll

the middle layer of cells in a leaf

photoautotroph

an organism capable of synthesizing its own food molecules (storing energy), using the energy of light

pigment

a molecule that is capable of absorbing light energy

stoma

the opening that regulates gas exchange and water regulation between leaves and the environment; plural: stomata

stroma

the fluid-filled space surrounding the grana inside a chloroplast where the Calvin cycle reactions of photosynthesis take place

thylakoid

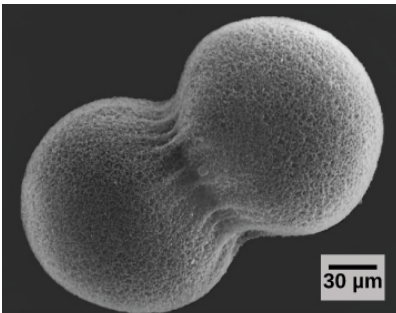
a disc-shaped membranous structure inside a chloroplast where the light-dependent reactions of photosynthesis take place using chlorophyll embedded in the membranes

Introduction

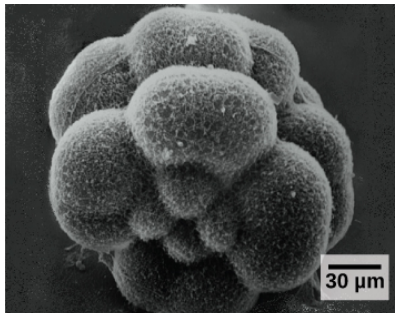
class="introduction"

A sea urchin begins life as a single cell that (a) divides to form two cells, visible by scanning electron microscopy. After four rounds of cell division, (b) there are 16 cells, as seen in this SEM image. After many rounds of cell division, the individual develops into a complex, multicellular organism, as seen in this (c) mature sea urchin. (credit a: modificatio

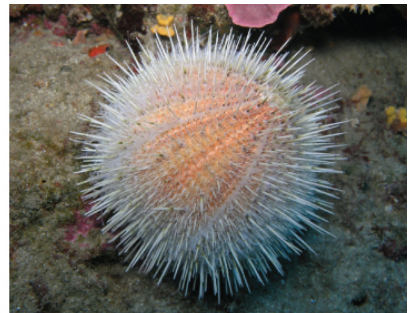
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(a)



(b)



(c)

The individual sexually reproducing organism—including humans—begins life as a fertilized egg, or zygote. Trillions of cell divisions subsequently occur in a controlled manner to produce a complex, multicellular human. In other words, that original single cell was the ancestor of every other cell in the body. Once a human individual is fully grown, cell reproduction is still

necessary to repair or regenerate tissues. For example, new blood and skin cells are constantly being produced. All multicellular organisms use cell division for growth, and in most cases, the maintenance and repair of cells and tissues. Single-celled organisms use cell division as their method of reproduction.

The Genome

By the end of this section, you will be able to:

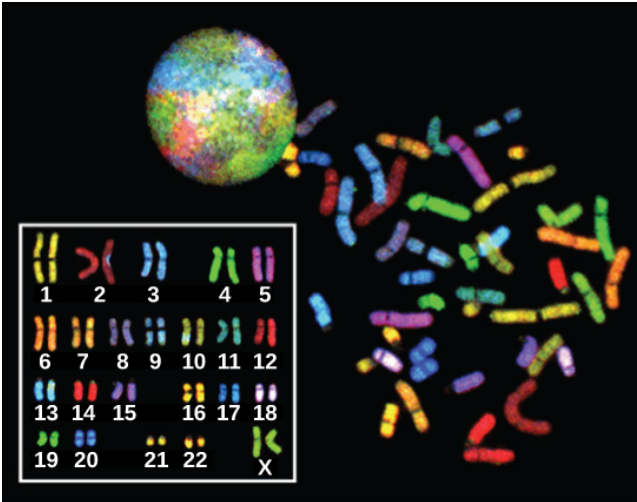
- Describe the prokaryotic and eukaryotic genome
- Distinguish between chromosomes, genes, and traits

The continuity of life from one cell to another has its foundation in the reproduction of cells by way of the cell cycle. The cell cycle is an orderly sequence of events in the life of a cell from the division of a single parent cell to produce two new daughter cells, to the subsequent division of those daughter cells. The mechanisms involved in the cell cycle are highly conserved across eukaryotes. Organisms as diverse as protists, plants, and animals employ similar steps.

Genomic DNA

Before discussing the steps a cell undertakes to replicate, a deeper understanding of the structure and function of a cell's genetic information is necessary. A cell's complete complement of DNA is called its **genome**. In prokaryotes, the genome is composed of a single, double-stranded DNA molecule in the form of a loop or circle. The region in the cell containing this genetic material is called a nucleoid. Some prokaryotes also have smaller loops of DNA called plasmids that are not essential for normal growth.

In eukaryotes, the genome comprises several double-stranded, linear DNA molecules ([\[link\]](#)) bound with proteins to form complexes called chromosomes. Each species of eukaryote has a characteristic number of chromosomes in the nuclei of its cells. Human body cells (somatic cells) have 46 chromosomes. A somatic cell contains two matched sets of chromosomes, a configuration known as **diploid**. The letter n is used to represent a single set of chromosomes; therefore a diploid organism is designated $2n$. Human cells that contain one set of 23 chromosomes are called **gametes**, or sex cells; these eggs and sperm are designated n , or **haploid**.



There are 23 pairs of homologous chromosomes in a female human somatic cell. These chromosomes are viewed within the nucleus (top), removed from a cell in mitosis (right), and arranged according to length (left) in an arrangement called a karyotype. In this image, the chromosomes were exposed to fluorescent stains to distinguish them. (credit: “718 Bot”/Wikimedia Commons, National Human Genome Research)

The matched pairs of chromosomes in a diploid organism are called **homologous chromosomes**. Homologous chromosomes are the same length and have specific nucleotide segments called **genes** in exactly the same location, or **locus**. Genes, the functional units of chromosomes, determine specific characteristics by coding for specific proteins. Traits are the different forms of a characteristic. For example, the shape of earlobes is a characteristic with traits of free or attached.

Each copy of the homologous pair of chromosomes originates from a different parent; therefore, the copies of each of the genes themselves may not be identical. The variation of individuals within a species is caused by the specific combination of the genes inherited from both parents. For example, there are three possible gene sequences on the human chromosome that codes for blood type: sequence A, sequence B, and sequence O. Because all diploid human cells have two copies of the chromosome that determines blood type, the blood type (the trait) is determined by which two versions of the marker gene are inherited. It is possible to have two copies of the same gene sequence, one on each homologous chromosome (for example, AA, BB, or OO), or two different sequences, such as AB.

Minor variations in traits such as those for blood type, eye color, and height contribute to the natural variation found within a species. The sex chromosomes, X and Y, are the single exception to the rule of homologous chromosomes; other than a small amount of homology that is necessary to reliably produce gametes, the genes found on the X and Y chromosomes are not the same.

Section Summary

Prokaryotes have a single loop chromosome, whereas eukaryotes have multiple, linear chromosomes surrounded by a nuclear membrane. Human somatic cells have 46 chromosomes consisting of two sets of 22 homologous chromosomes and a pair of nonhomologous sex chromosomes. This is the $2n$, or diploid, state. Human gametes have 23 chromosomes or one complete set of chromosomes. This is the n , or haploid, state. Genes are segments of DNA that code for a specific protein or RNA molecule. An organism's traits are determined in large part by the genes inherited from each parent, but also by the environment that they experience. Genes are expressed as characteristics of the organism and each characteristic may have different variants called traits that are caused by differences in the DNA sequence for a gene.

Multiple Choice

Exercise:**Problem:**

A diploid cell has _____ the number of chromosomes as a haploid cell.

- a. one-fourth
- b. one-half
- c. twice
- d. four times

Solution:

C

Exercise:**Problem:**

An organism's traits are determined by the specific combination of inherited _____.

- a. cells
- b. genes
- c. proteins
- d. chromatids

Solution:

B

Free Response**Exercise:**

Problem:

Compare and contrast a human somatic cell to a human gamete.

Solution:

Human somatic cells have 46 chromosomes, including 22 homologous pairs and one pair of nonhomologous sex chromosomes. This is the $2n$, or diploid, condition. Human gametes have 23 chromosomes, one each of 23 unique chromosomes. This is the n , or haploid, condition.

Glossary**diploid**

describes a cell, nucleus, or organism containing two sets of chromosomes ($2n$)

gamete

a haploid reproductive cell or sex cell (sperm or egg)

gene

the physical and functional unit of heredity; a sequence of DNA that codes for a specific peptide or RNA molecule

genome

the entire genetic complement (DNA) of an organism

haploid

describes a cell, nucleus, or organism containing one set of chromosomes (n)

homologous chromosomes

chromosomes of the same length with genes in the same location; diploid organisms have pairs of homologous chromosomes, and the members of each pair come from different parents

locus

the position of a gene on a chromosome

Cancer and the Cell Cycle

By the end of this section, you will be able to:

- Explain how cancer is caused by uncontrolled cell division
- Understand how proto-oncogenes are normal cell genes that, when mutated, become oncogenes
- Describe how tumor suppressors function to stop the cell cycle until certain events are completed
- Explain how mutant tumor suppressors cause cancer

Cancer is a collective name for many different diseases caused by a common mechanism: uncontrolled cell division. Despite the redundancy and overlapping levels of cell-cycle control, errors occur. One of the critical processes monitored by the cell-cycle checkpoint surveillance mechanism is the proper replication of DNA during the S phase. Even when all of the cell-cycle controls are fully functional, a small percentage of replication errors (mutations) will be passed on to the daughter cells. If one of these changes to the DNA nucleotide sequence occurs within a gene, a gene mutation results. All cancers begin when a gene mutation gives rise to a faulty protein that participates in the process of cell reproduction. The change in the cell that results from the malformed protein may be minor. Even minor mistakes, however, may allow subsequent mistakes to occur more readily. Over and over, small, uncorrected errors are passed from parent cell to daughter cells and accumulate as each generation of cells produces more non-functional proteins from uncorrected DNA damage. Eventually, the pace of the cell cycle speeds up as the effectiveness of the control and repair mechanisms decreases. Uncontrolled growth of the mutated cells outpaces the growth of normal cells in the area, and a tumor can result.

Proto-oncogenes

The genes that code for the positive cell-cycle regulators are called **proto-oncogenes**. Proto-oncogenes are normal genes that, when mutated, become **oncogenes**—genes that cause a cell to become cancerous. Consider what might happen to the cell cycle in a cell with a recently acquired oncogene. In most instances, the alteration of the DNA sequence will result in a less

functional (or non-functional) protein. The result is detrimental to the cell and will likely prevent the cell from completing the cell cycle; however, the organism is not harmed because the mutation will not be carried forward. If a cell cannot reproduce, the mutation is not propagated and the damage is minimal. Occasionally, however, a gene mutation causes a change that increases the activity of a positive regulator. For example, a mutation that allows Cdk, a protein involved in cell-cycle regulation, to be activated before it should be could push the cell cycle past a checkpoint before all of the required conditions are met. If the resulting daughter cells are too damaged to undertake further cell divisions, the mutation would not be propagated and no harm comes to the organism. However, if the atypical daughter cells are able to divide further, the subsequent generation of cells will likely accumulate even more mutations, some possibly in additional genes that regulate the cell cycle.

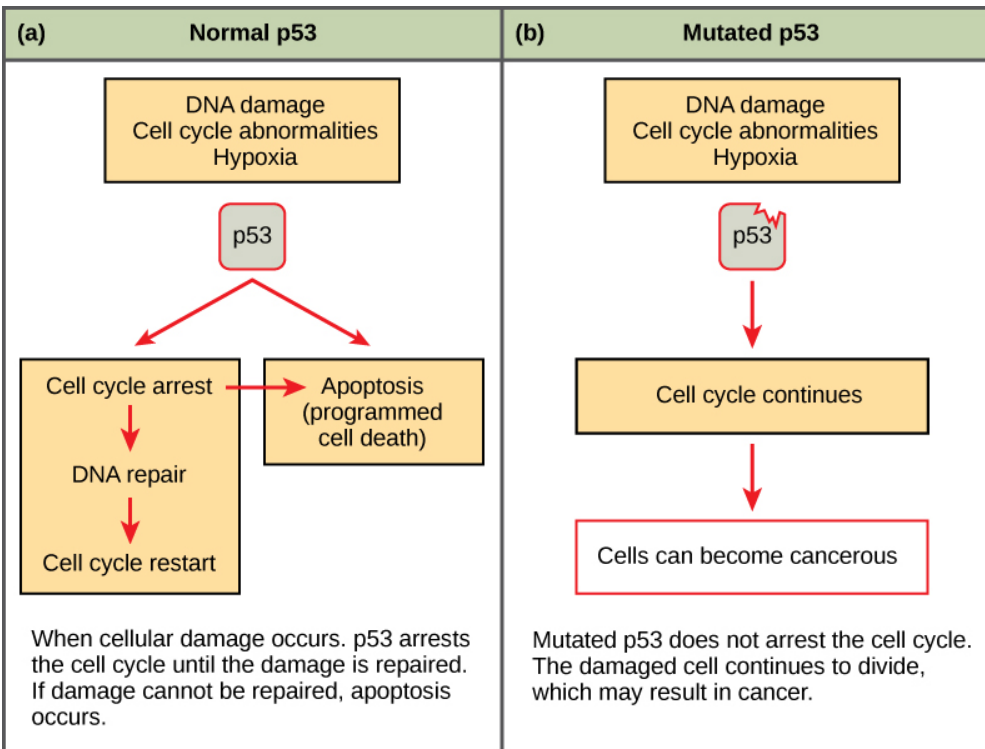
The Cdk example is only one of many genes that are considered proto-oncogenes. In addition to the cell-cycle regulatory proteins, any protein that influences the cycle can be altered in such a way as to override cell-cycle checkpoints. Once a proto-oncogene has been altered such that there is an increase in the rate of the cell cycle, it is then called an oncogene.

Tumor Suppressor Genes

Like proto-oncogenes, many of the negative cell-cycle regulatory proteins were discovered in cells that had become cancerous. **Tumor suppressor genes** are genes that code for the negative regulator proteins, the type of regulator that—when activated—can prevent the cell from undergoing uncontrolled division. The collective function of the best-understood tumor suppressor gene proteins, retinoblastoma protein (RB1), p53, and p21, is to put up a roadblock to cell-cycle progress until certain events are completed. A cell that carries a mutated form of a negative regulator might not be able to halt the cell cycle if there is a problem.

Mutated p53 genes have been identified in more than half of all human tumor cells. This discovery is not surprising in light of the multiple roles that the p53 protein plays at the G₁ checkpoint. The p53 protein activates other genes whose products halt the cell cycle (allowing time for DNA

repair), activates genes whose products participate in DNA repair, or activates genes that initiate cell death when DNA damage cannot be repaired. A damaged p53 gene can result in the cell behaving as if there are no mutations ([link](#)). This allows cells to divide, propagating the mutation in daughter cells and allowing the accumulation of new mutations. In addition, the damaged version of p53 found in cancer cells cannot trigger cell death.



(a) The role of p53 is to monitor DNA. If damage is detected, p53 triggers repair mechanisms. If repairs are unsuccessful, p53 signals apoptosis. (b) A cell with an abnormal p53 protein cannot repair damaged DNA and cannot signal apoptosis. Cells with abnormal p53 can become cancerous. (credit: modification of work by Thierry Soussi)

Note:**Concept in Action**

Go to [this website](#) to watch an animation of how cancer results from errors in the cell cycle.

Section Summary

Cancer is the result of unchecked cell division caused by a breakdown of the mechanisms regulating the cell cycle. The loss of control begins with a change in the DNA sequence of a gene that codes for one of the regulatory molecules. Faulty instructions lead to a protein that does not function as it should. Any disruption of the monitoring system can allow other mistakes to be passed on to the daughter cells. Each successive cell division will give rise to daughter cells with even more accumulated damage. Eventually, all checkpoints become nonfunctional, and rapidly reproducing cells crowd out normal cells, resulting in tumorous growth.

Multiple Choice**Exercise:****Problem:**

_____ are changes to the nucleotides in a segment of DNA that codes for a protein.

- a. Proto-oncogenes
- b. Tumor suppressor genes
- c. Gene mutations

d. Negative regulators

Solution:

C

Exercise:

Problem:

A gene that codes for a positive cell cycle regulator is called a(n)
_____.

- a. kinase inhibitor
- b. tumor suppressor gene
- c. proto-oncogene
- d. oncogene

Solution:

C

Free Response

Exercise:

Problem: Outline the steps that lead to a cell becoming cancerous.

Solution:

If one of the genes that produce regulator proteins becomes mutated, it produces a malformed, possibly non-functional, cell-cycle regulator. This increases the chance that more mutations will be left unrepaired in the cell. Each subsequent generation of cells sustains more damage. The cell cycle can speed up as a result of loss of functional checkpoint proteins. The cells can lose the ability to self-destruct.

Exercise:**Problem:**

Explain the difference between a proto-oncogene and a tumor suppressor gene.

Solution:

A proto-oncogene is the segment of DNA that codes for one of the positive cell-cycle regulators. If that gene becomes mutated to a form that is overactive, it is considered an oncogene. A tumor suppressor gene is a segment of DNA that codes for one of the negative cell-cycle regulators. If that gene becomes mutated to a form that is underactive, the cell cycle will run unchecked.

Glossary**oncogene**

a mutated version of a proto-oncogene, which allows for uncontrolled progression of the cell cycle, or uncontrolled cell reproduction

proto-oncogene

a normal gene that controls cell division by regulating the cell cycle that becomes an oncogene if it is mutated

tumor suppressor gene

a gene that codes for regulator proteins that prevent the cell from undergoing uncontrolled division

Introduction

class="introduction"

Each of us,
like these
other large
multicellula
r organisms,
begins life
as a
fertilized
egg. After
trillions of
cell
divisions,
each of us
develops
into a
complex,
multicellula
r organism.
(credit a:
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USGS;
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by Martin
Pettitt)



(a)

(b)

(c)

The ability to reproduce *in kind* is a basic characteristic of all living things. *In kind* means that the offspring of any organism closely resembles its parent or parents. Hippopotamuses give birth to hippopotamus calves; Monterey pine trees produce seeds from which Monterey pine seedlings emerge; and adult flamingos lay eggs that hatch into flamingo chicks. *In kind* does not generally mean *exactly the same*. While many single-celled organisms and a few multicellular organisms can produce genetically identical clones of themselves through mitotic cell division, many single-celled organisms and most multicellular organisms reproduce regularly using another method.

Sexual reproduction is the production by parents of haploid cells and the fusion of a haploid cell from each parent to form a single, unique diploid cell. In multicellular organisms, the new diploid cell will then undergo mitotic cell divisions to develop into an adult organism. A type of cell division called meiosis leads to the haploid cells that are part of the sexual reproductive cycle. Sexual reproduction, specifically meiosis and fertilization, introduces variation into offspring that may account for the evolutionary success of sexual reproduction. The vast majority of eukaryotic organisms can or must employ some form of meiosis and fertilization to reproduce.

Sexual Reproduction

By the end of this section, you will be able to:

- Explain that variation among offspring is a potential evolutionary advantage resulting from sexual reproduction
- Describe the three different life-cycle strategies among sexual multicellular organisms and their commonalities

Sexual reproduction was an early evolutionary innovation after the appearance of eukaryotic cells. The fact that most eukaryotes reproduce sexually is evidence of its evolutionary success. In many animals, it is the only mode of reproduction. And yet, scientists recognize some real disadvantages to sexual reproduction. On the surface, offspring that are genetically identical to the parent may appear to be more advantageous. If the parent organism is successfully occupying a habitat, offspring with the same traits would be similarly successful. There is also the obvious benefit to an organism that can produce offspring by asexual budding, fragmentation, or asexual eggs. These methods of reproduction do not require another organism of the opposite sex. There is no need to expend energy finding or attracting a mate. That energy can be spent on producing more offspring. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, asexual populations only have female individuals, so every individual is capable of reproduction. In contrast, the males in sexual populations (half the population) are not producing offspring themselves. Because of this, an asexual population can grow twice as fast as a sexual population in theory. This means that in competition, the asexual population would have the advantage. All of these advantages to asexual reproduction, which are also disadvantages to sexual reproduction, should mean that the number of species with asexual reproduction should be more common.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why is sexual reproduction so common? This is one of the important questions in biology and has been the focus of much research from the latter half of the twentieth century until now. A likely explanation is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of those

offspring. The only source of variation in asexual organisms is mutation. This is the ultimate source of variation in sexual organisms. In addition, those different mutations are continually reshuffled from one generation to the next when different parents combine their unique genomes, and the genes are mixed into different combinations by the process of **meiosis**. Meiosis is the division of the contents of the nucleus that divides the chromosomes among gametes. Variation is introduced during meiosis, as well as when the gametes combine in fertilization.

Note:

Evolution in Action

The Red Queen Hypothesis

There is no question that sexual reproduction provides evolutionary advantages to organisms that employ this mechanism to produce offspring. The problematic question is why, even in the face of fairly stable conditions, sexual reproduction persists when it is more difficult and produces fewer offspring for individual organisms? Variation is the outcome of sexual reproduction, but why are ongoing variations necessary? Enter the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973. [\[footnote\]](#) The concept was named in reference to the Red Queen's race in Lewis Carroll's book, *Through the Looking-Glass*, in which the Red Queen says one must run at full speed just to stay where one is.

Leigh Van Valen, "A new evolutionary law," *Evolutionary Theory* 1 (1973): 1–30.

All species coevolve with other organisms. For example, predators coevolve with their prey, and parasites coevolve with their hosts. A remarkable example of coevolution between predators and their prey is the unique coadaptation of night flying bats and their moth prey. Bats find their prey by emitting high-pitched clicks, but moths have evolved simple ears to hear these clicks so they can avoid the bats. The moths have also adapted behaviors, such as flying away from the bat when they first hear it, or dropping suddenly to the ground when the bat is upon them. Bats have evolved "quiet" clicks in an attempt to evade the moth's hearing. Some moths have evolved the ability to respond to the bats' clicks with their own clicks as a strategy to confuse the bats echolocation abilities.

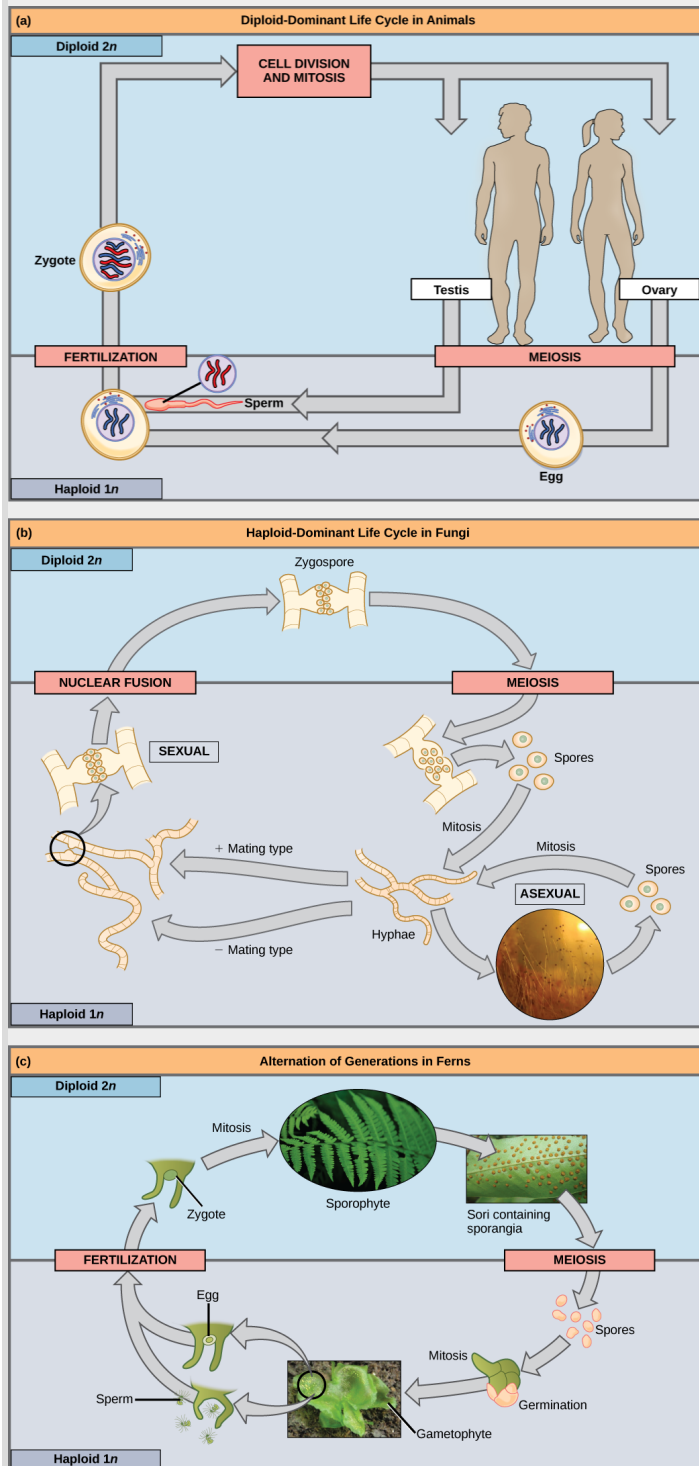
Each tiny advantage gained by favorable variation gives a species an edge over close competitors, predators, parasites, or even prey. The only method that will allow a coevolving species to keep its own share of the resources is also to continually improve its ability to survive and produce offspring. As one species gains an advantage, other species must also develop an advantage or they will be outcompeted. No single species progresses too far ahead because genetic variation among progeny of sexual reproduction provides all species with a mechanism to produce adapted individuals. Species whose individuals cannot keep up become extinct. The Red Queen's catchphrase was, "It takes all the running you can do to stay in the same place." This is an apt description of coevolution between competing species.

Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual **life cycles**. What happens between these two events depends on the organism. The process of meiosis reduces the resulting gamete's chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. There are three main categories of life cycles in multicellular organisms: **diploid-dominant**, in which the multicellular diploid stage is the most obvious life stage (and there is no multicellular haploid stage), as with most animals including humans; **haploid-dominant**, in which the multicellular haploid stage is the most obvious life stage (and there is no multicellular diploid stage), as with all fungi and some algae; and **alternation of generations**, in which the two stages, haploid and diploid, are apparent to one degree or another depending on the group, as with plants and some algae.

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. The gametes are produced from diploid **germ cells**, a special cell line that only produces gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state ([link](#)a).

Note:
Art Connection



(a) In animals, sexually reproducing adults form haploid gametes from

diploid germ cells. (b) Fungi, such as black bread mold (*Rhizopus nigricans*), have haploid-dominant life cycles. (c) Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. (credit c “fern”: modification of work by Cory Zanker; credit c “gametophyte”: modification of work by “Vlmastra”/Wikimedia Commons)

If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Most fungi and algae employ a life-cycle strategy in which the multicellular “body” of the organism is haploid. During sexual reproduction, specialized haploid cells from two individuals join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called spores ([link](#)b).

The third life-cycle type, employed by some algae and all plants, is called alternation of generations. These species have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called **gametophytes** because they produce gametes. Meiosis is not involved in the production of gametes in this case, as the organism that produces gametes is already haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a **sporophyte**. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will develop into the gametophytes ([link](#)c).

Section Summary

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces genetically unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition. Thus, sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and alternation of generations, demonstrated by plants and some algae.

Art Connections

Exercise:

Problem:

[\[link\]](#) If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Solution:

[\[link\]](#) Yes, it will be able to reproduce asexually.

Multiple Choice

Exercise:

Problem:

What is a likely evolutionary advantage of sexual reproduction over asexual reproduction?

- a. sexual reproduction involves fewer steps
- b. less chance of using up the resources in a given environment

- c. sexual reproduction results in greater variation in the offspring
 - d. sexual reproduction is more cost-effective
-

Solution:

C

Exercise:

Problem:

Which type of life cycle has both a haploid and diploid multicellular stage?

- a. an asexual life cycle
 - b. diploid-dominant
 - c. haploid-dominant
 - d. alternation of generations
-

Solution:

D

Exercise:

Problem: Which event leads to a diploid cell in a life cycle?

- a. meiosis
 - b. fertilization
 - c. alternation of generations
 - d. mutation
-

Solution:

B

Free Response

Exercise:

Problem:

Explain the advantage that populations of sexually reproducing organisms have over asexually reproducing organisms?

Solution:

The offspring of sexually reproducing organisms are all genetically unique. Because of this, sexually reproducing organisms may have more successful survival of offspring in environments that change than asexually reproducing organisms, whose offspring are all genetically identical. In addition, the rate of adaptation of sexually reproducing organisms is higher, because of their increased variation. This may allow sexually reproducing organisms to adapt more quickly to competitors and parasites, who are evolving new ways to exploit or outcompete them.

Exercise:

Problem:

Describe the two events that are common to all sexually reproducing organisms and how they fit into the different life cycles of those organisms.

Solution:

The two events common to all sexually reproducing organisms are meiosis and fertilization. Meiosis reduces a diploid cell to a haploid state. The haploid cell may divide mitotically to produce an organism, some of whose cells will combine during fertilization, or the haploid cells produced by meiosis may immediately combine in fertilization to produce a diploid cell that divides to produce an organism.

Glossary

alternation of generations

a life-cycle type in which the diploid and haploid stages alternate

diploid-dominant

a life-cycle type in which the multicellular diploid stage is prevalent

haploid-dominant

a life-cycle type in which the multicellular haploid stage is prevalent

gametophyte

a multicellular haploid life-cycle stage that produces gametes

germ cell

a specialized cell that produces gametes, such as eggs or sperm

life cycle

the sequence of events in the development of an organism and the production of cells that produce offspring

meiosis

a nuclear division process that results in four haploid cells

sporophyte

a multicellular diploid life-cycle stage that produces spores

Introduction

class="introduction"

Experimentin
g with
thousands of
garden peas,
Mendel
uncovered the
fundamentals
of genetics.
(credit:
modification
of work by
Jerry
Kirkhart)



Genetics is the study of heredity. Johann Gregor Mendel set the framework for genetics long before chromosomes or genes had been identified, at a time when meiosis was not well understood. Mendel selected a simple biological system and conducted methodical, quantitative analyses using large sample sizes. Because of Mendel's work, the fundamental principles of heredity were revealed. We now know that genes, carried on chromosomes, are the basic functional units of heredity with the ability to be replicated, expressed, or mutated. Today, the postulates put forth by Mendel form the basis of classical, or Mendelian, genetics. Not all genes are transmitted from parents to offspring according to Mendelian genetics, but Mendel's experiments serve as an excellent starting point for thinking about inheritance.

Mendel's Experiments

By the end of this section, you will be able to:

- Explain the scientific reasons for the success of Mendel's experimental work
- Describe the expected outcomes of monohybrid crosses involving dominant and recessive alleles



Johann Gregor Mendel
set the framework for
the study of genetics.

Johann Gregor Mendel (1822–1884) ([link](#)) was a lifelong learner, teacher, scientist, and man of faith. As a young adult, he joined the Augustinian Abbey of St. Thomas in Brno in what is now the Czech Republic. Supported by the monastery, he taught physics, botany, and natural science courses at the secondary and university levels. In 1856, he began a decade-long research pursuit involving inheritance patterns in honeybees and plants, ultimately settling on pea plants as his primary **model system** (a system with convenient characteristics that is used to study a specific biological phenomenon to gain understanding to be applied to other systems). In 1865, Mendel presented the results of his experiments with nearly 30,000 pea plants to the local natural history society. He

demonstrated that traits are transmitted faithfully from parents to offspring in specific patterns. In 1866, he published his work, *Experiments in Plant Hybridization*,^[footnote] in the proceedings of the Natural History Society of Brunn.

Johann Gregor Mendel, “Versuche über Pflanzenhybriden.” *Verhandlungen des naturforschenden Vereines in Brunn*, Bd. IV für das Jahr, 1865 Abhandlungen (1866):3–47. [for English translation, see <http://www.mendelweb.org/Mendel.plain.html>]

Mendel’s work went virtually unnoticed by the scientific community, which incorrectly believed that the process of inheritance involved a blending of parental traits that produced an intermediate physical appearance in offspring. This hypothetical process appeared to be correct because of what we know now as continuous variation. **Continuous variation** is the range of small differences we see among individuals in a characteristic like human height. It does appear that offspring are a “blend” of their parents’ traits when we look at characteristics that exhibit continuous variation. Mendel worked instead with traits that show **discontinuous variation**. Discontinuous variation is the variation seen among individuals when each individual shows one of two—or a very few—easily distinguishable traits, such as violet or white flowers. Mendel’s choice of these kinds of traits allowed him to see experimentally that the traits were not blended in the offspring as would have been expected at the time, but that they were inherited as distinct traits. In 1868, Mendel became abbot of the monastery and exchanged his scientific pursuits for his pastoral duties. He was not recognized for his extraordinary scientific contributions during his lifetime; in fact, it was not until 1900 that his work was rediscovered, reproduced, and revitalized by scientists on the brink of discovering the chromosomal basis of heredity.

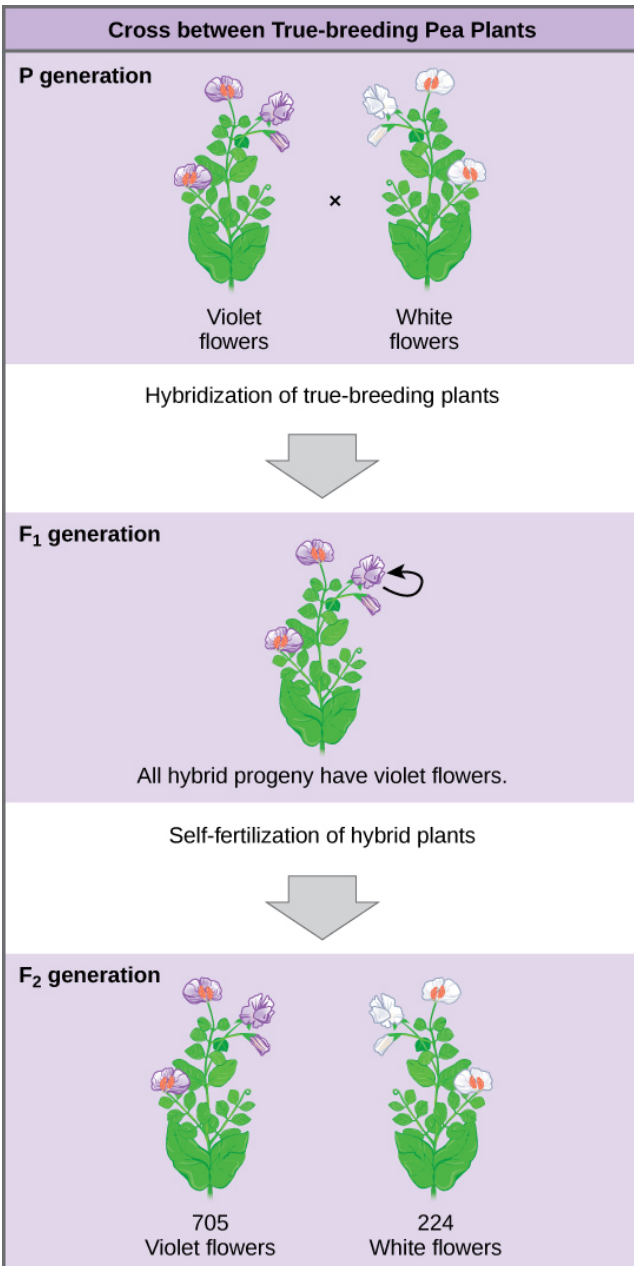
Mendel’s Crosses

Mendel’s seminal work was accomplished using the garden pea, *Pisum sativum*, to study inheritance. This species naturally self-fertilizes, meaning that pollen encounters ova within the same flower. The flower petals remain sealed tightly until pollination is completed to prevent the pollination of other plants. The result is highly inbred, or “true-breeding,” pea plants.

These are plants that always produce offspring that look like the parent. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected traits in offspring that might occur if the plants were not true breeding. The garden pea also grows to maturity within one season, meaning that several generations could be evaluated over a relatively short time. Finally, large quantities of garden peas could be cultivated simultaneously, allowing Mendel to conclude that his results did not come about simply by chance.

Mendel performed **hybridizations**, which involve mating two true-breeding individuals that have different traits. In the pea, which is naturally self-pollinating, this is done by manually transferring pollen from the anther of a mature pea plant of one variety to the stigma of a separate mature pea plant of the second variety.

Plants used in first-generation crosses were called **P**, or parental generation, plants ([\[link\]](#)). Mendel collected the seeds produced by the P plants that resulted from each cross and grew them the following season. These offspring were called the **F₁**, or the first filial (filial = daughter or son), generation. Once Mendel examined the characteristics in the F₁ generation of plants, he allowed them to self-fertilize naturally. He then collected and grew the seeds from the F₁ plants to produce the **F₂**, or second filial, generation. Mendel's experiments extended beyond the F₂ generation to the F₃ generation, F₄ generation, and so on, but it was the ratio of characteristics in the P, F₁, and F₂ generations that were the most intriguing and became the basis of Mendel's postulates.



Mendel's process for performing crosses included examining flower color.

Garden Pea Characteristics Revealed the Basics of Heredity

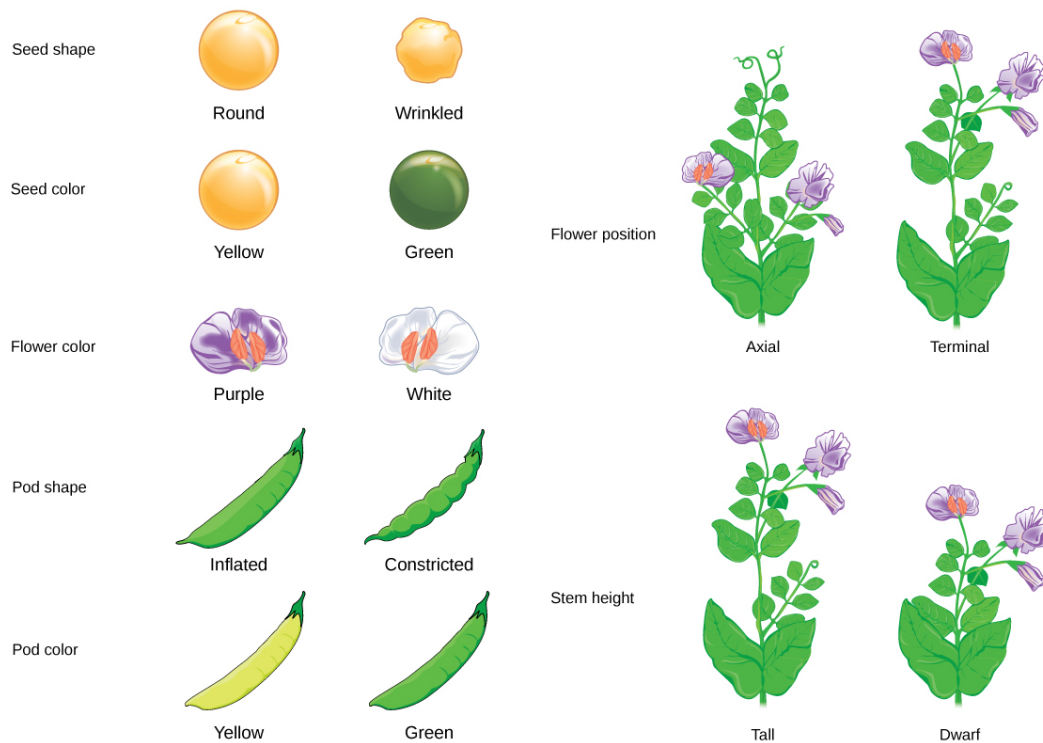
In his 1865 publication, Mendel reported the results of his crosses involving seven different characteristics, each with two contrasting traits. A **trait** is defined as a variation in the physical appearance of a heritable characteristic. The characteristics included plant height, seed texture, seed color, flower color, pea-pod size, pea-pod color, and flower position. For the characteristic of flower color, for example, the two contrasting traits were white versus violet. To fully examine each characteristic, Mendel generated large numbers of F_1 and F_2 plants and reported results from thousands of F_2 plants.

What results did Mendel find in his crosses for flower color? First, Mendel confirmed that he was using plants that bred true for white or violet flower color. Irrespective of the number of generations that Mendel examined, all self-crossed offspring of parents with white flowers had white flowers, and all self-crossed offspring of parents with violet flowers had violet flowers. In addition, Mendel confirmed that, other than flower color, the pea plants were physically identical. This was an important check to make sure that the two varieties of pea plants only differed with respect to one trait, flower color.

Once these validations were complete, Mendel applied the pollen from a plant with violet flowers to the stigma of a plant with white flowers. After gathering and sowing the seeds that resulted from this cross, Mendel found that 100 percent of the F_1 hybrid generation had violet flowers. Conventional wisdom at that time would have predicted the hybrid flowers to be pale violet or for hybrid plants to have equal numbers of white and violet flowers. In other words, the contrasting parental traits were expected to blend in the offspring. Instead, Mendel's results demonstrated that the white flower trait had completely disappeared in the F_1 generation.

Importantly, Mendel did not stop his experimentation there. He allowed the F_1 plants to self-fertilize and found that 705 plants in the F_2 generation had violet flowers and 224 had white flowers. This was a ratio of 3.15 violet flowers to one white flower, or approximately 3:1. When Mendel transferred pollen from a plant with violet flowers to the stigma of a plant with white flowers and vice versa, he obtained approximately the same ratio irrespective of which parent—male or female—contributed which trait.

This is called a **reciprocal cross**—a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross. For the other six characteristics that Mendel examined, the F_1 and F_2 generations behaved in the same way that they behaved for flower color. One of the two traits would disappear completely from the F_1 generation, only to reappear in the F_2 generation at a ratio of roughly 3:1 ([link](#)).



Mendel identified seven pea plant characteristics.

Upon compiling his results for many thousands of plants, Mendel concluded that the characteristics could be divided into expressed and latent traits. He called these dominant and recessive traits, respectively.

Dominant traits are those that are inherited unchanged in a hybridization.

Recessive traits become latent, or disappear in the offspring of a hybridization. The recessive trait does, however, reappear in the progeny of

the hybrid offspring. An example of a dominant trait is the violet-colored flower trait. For this same characteristic (flower color), white-colored flowers are a recessive trait. The fact that the recessive trait reappeared in the F_2 generation meant that the traits remained separate (and were not blended) in the plants of the F_1 generation. Mendel proposed that this was because the plants possessed two copies of the trait for the flower-color characteristic, and that each parent transmitted one of their two copies to their offspring, where they came together. Moreover, the physical observation of a dominant trait could mean that the genetic composition of the organism included two dominant versions of the characteristic, or that it included one dominant and one recessive version. Conversely, the observation of a recessive trait meant that the organism lacked any dominant versions of this characteristic.

Note:**Concept in Action**

For an excellent review of Mendel's experiments and to perform your own crosses and identify patterns of inheritance, visit the [Mendel's Peas](#) web lab.

Section Summary

Working with garden pea plants, Mendel found that crosses between parents that differed for one trait produced F_1 offspring that all expressed one parent's traits. The traits that were visible in the F_1 generation are referred to as dominant, and traits that disappear in the F_1 generation are described as recessive. When the F_1 plants in Mendel's experiment were self-crossed,

the F_2 offspring exhibited the dominant trait or the recessive trait in a 3:1 ratio, confirming that the recessive trait had been transmitted faithfully from the original P parent. Reciprocal crosses generated identical F_1 and F_2 offspring ratios. By examining sample sizes, Mendel showed that traits were inherited as independent events.

Multiple Choice

Exercise:

Problem:

Imagine that you are performing a cross involving seed color in garden pea plants. What traits would you expect to observe in the F_1 offspring if you cross true-breeding parents with green seeds and yellow seeds? Yellow seed color is dominant over green.

- a. only yellow-green seeds
- b. only yellow seeds
- c. 1:1 yellow seeds:green seeds
- d. 1:3 green seeds:yellow seeds

Solution:

B

Exercise:

Problem:

Imagine that you are performing a cross involving seed texture in garden pea plants. You cross true-breeding round and wrinkled parents to obtain F_1 offspring. Which of the following experimental results in terms of numbers of plants are closest to what you expect in the F_2 progeny?

- a. 810 round seeds
- b. 810 wrinkled seeds

- c. 405:395 round seeds:wrinkled seeds
 - d. 610:190 round seeds:wrinkled seeds
-

Solution:

D

Free Response

Exercise:

Problem:

Describe one of the reasons that made the garden pea an excellent choice of model system for studying inheritance.

Solution:

The garden pea has flowers that close tightly during self-pollination. This helps to prevent accidental or unintentional fertilizations that could have diminished the accuracy of Mendel's data.

Glossary

continuous variation

a variation in a characteristic in which individuals show a range of traits with small differences between them

discontinuous variation

a variation in a characteristic in which individuals show two, or a few, traits with large differences between them

dominant

describes a trait that masks the expression of another trait when both versions of the gene are present in an individual

F_1

the first filial generation in a cross; the offspring of the parental generation

F_2

the second filial generation produced when F_1 individuals are self-crossed or fertilized with each other

hybridization

the process of mating two individuals that differ, with the goal of achieving a certain characteristic in their offspring

model system

a species or biological system used to study a specific biological phenomenon to gain understanding that will be applied to other species

P

the parental generation in a cross

recessive

describes a trait whose expression is masked by another trait when the alleles for both traits are present in an individual

reciprocal cross

a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross

trait

a variation in an inherited characteristic

Laws of Inheritance

By the end of this section, you will be able to:

- Explain the relationship between genotypes and phenotypes in dominant and recessive gene systems
- Use a Punnett square to calculate the expected proportions of genotypes and phenotypes in a monohybrid cross
- Explain Mendel's law of segregation and independent assortment in terms of genetics and the events of meiosis
- Explain the purpose and methods of a test cross

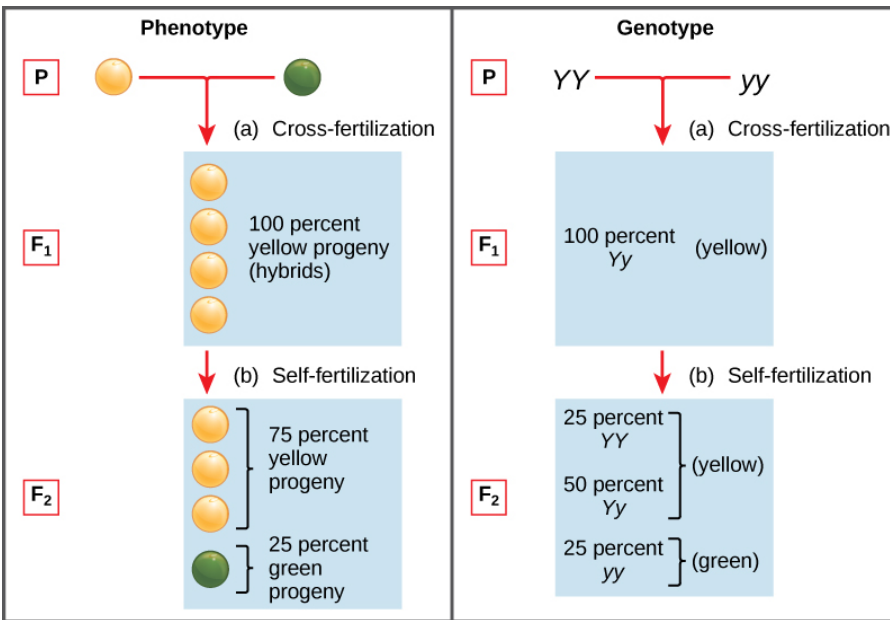
The seven characteristics that Mendel evaluated in his pea plants were each expressed as one of two versions, or traits. Mendel deduced from his results that each individual had two discrete copies of the characteristic that are passed individually to offspring. We now call those two copies genes, which are carried on chromosomes. The reason we have two copies of each gene is that we inherit one from each parent. In fact, it is the chromosomes we inherit and the two copies of each gene are located on paired chromosomes. Recall that in meiosis these chromosomes are separated out into haploid gametes. This separation, or segregation, of the homologous chromosomes means also that only one of the copies of the gene gets moved into a gamete. The offspring are formed when that gamete unites with one from another parent and the two copies of each gene (and chromosome) are restored.

For cases in which a single gene controls a single characteristic, a diploid organism has two genetic copies that may or may not encode the same version of that characteristic. For example, one individual may carry a gene that determines white flower color and a gene that determines violet flower color. Gene variants that arise by mutation and exist at the same relative locations on homologous chromosomes are called **alleles**. Mendel examined the inheritance of genes with just two allele forms, but it is common to encounter more than two alleles for any given gene in a natural population.

Phenotypes and Genotypes

Two alleles for a given gene in a diploid organism are expressed and interact to produce physical characteristics. The observable traits expressed by an organism are referred to as its **phenotype**. An organism's underlying genetic makeup, consisting of both the physically visible and the non-expressed alleles, is called its **genotype**. Mendel's hybridization experiments demonstrate the difference between phenotype and genotype. For example, the phenotypes that Mendel observed in his crosses between pea plants with differing traits are connected to the diploid genotypes of the plants in the P, F₁, and F₂ generations. We will use a second trait that Mendel investigated, seed color, as an example. Seed color is governed by a single gene with two alleles. The yellow-seed allele is dominant and the green-seed allele is recessive. When true-breeding plants were cross-fertilized, in which one parent had yellow seeds and one had green seeds, all of the F₁ hybrid offspring had yellow seeds. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with yellow seeds. However, we know that the allele donated by the parent with green seeds was not simply lost because it reappeared in some of the F₂ offspring ([link](#)). Therefore, the F₁ plants must have been genotypically different from the parent with yellow seeds.

The P plants that Mendel used in his experiments were each homozygous for the trait he was studying. Diploid organisms that are **homozygous** for a gene have two identical alleles, one on each of their homologous chromosomes. The genotype is often written as YY or yy, for which each letter represents one of the two alleles in the genotype. The dominant allele is capitalized and the recessive allele is lower case. The letter used for the gene (seed color in this case) is usually related to the dominant trait (yellow allele, in this case, or "Y"). Mendel's parental pea plants always bred true because both produced gametes carried the same allele. When P plants with contrasting traits were cross-fertilized, all of the offspring were **heterozygous** for the contrasting trait, meaning their genotype had different alleles for the gene being examined. For example, the F₁ yellow plants that received a Y allele from their yellow parent and a y allele from their green parent had the genotype Yy.



Phenotypes are physical expressions of traits that are transmitted by alleles. Capital letters represent dominant alleles and lowercase letters represent recessive alleles. The phenotypic ratios are the ratios of visible characteristics. The genotypic ratios are the ratios of gene combinations in the offspring, and these are not always distinguishable in the phenotypes.

Law of Dominance

Our discussion of homozygous and heterozygous organisms brings us to why the F₁ heterozygous offspring were identical to one of the parents, rather than expressing both alleles. In all seven pea-plant characteristics, one of the two contrasting alleles was dominant, and the other was recessive. Mendel called the dominant allele the expressed unit factor; the recessive allele was referred to as the latent unit factor. We now know that these so-called unit factors are actually genes on homologous chromosomes. For a gene that is expressed in a dominant and recessive

pattern, homozygous dominant and heterozygous organisms will look identical (that is, they will have different genotypes but the same phenotype), and the recessive allele will only be observed in homozygous recessive individuals ([\[link\]](#)).

Correspondence between Genotype and Phenotype for a Dominant-Recessive Characteristic.			
	Homozygous	Heterozygous	Homozygous
Genotype	YY	Yy	yy
Phenotype	yellow	yellow	green

Mendel’s **law of dominance** states that in a heterozygote, one trait will conceal the presence of another trait for the same characteristic. For example, when crossing true-breeding violet-flowered plants with true-breeding white-flowered plants, all of the offspring were violet-flowered, even though they all had one allele for violet and one allele for white. Rather than both alleles contributing to a phenotype, the dominant allele will be expressed exclusively. The recessive allele will remain latent, but will be transmitted to offspring in the same manner as that by which the dominant allele is transmitted. The recessive trait will only be expressed by offspring that have two copies of this allele ([\[link\]](#)), and these offspring will breed true when self-crossed.



The allele for albinism, expressed here in humans, is recessive. Both of this child's parents carried the recessive allele.

Monohybrid Cross and the Punnett Square

When fertilization occurs between two true-breeding parents that differ by only the characteristic being studied, the process is called a **monohybrid** cross, and the resulting offspring are called monohybrids. Mendel performed seven types of monohybrid crosses, each involving contrasting traits for different characteristics. Out of these crosses, all of the F_1 offspring had the phenotype of one parent, and the F_2 offspring had a 3:1 phenotypic ratio. On the basis of these results, Mendel postulated that each parent in the monohybrid cross contributed one of two paired unit factors to each offspring, and every possible combination of unit factors was equally likely.

The results of Mendel's research can be explained in terms of probabilities, which are mathematical measures of likelihood. The probability of an event is calculated by the number of times the event occurs divided by the total number of opportunities for the event to occur. A probability of one (100 percent) for some event indicates that it is guaranteed to occur, whereas a probability of zero (0 percent) indicates that it is guaranteed to not occur, and a probability of 0.5 (50 percent) means it has an equal chance of occurring or not occurring.

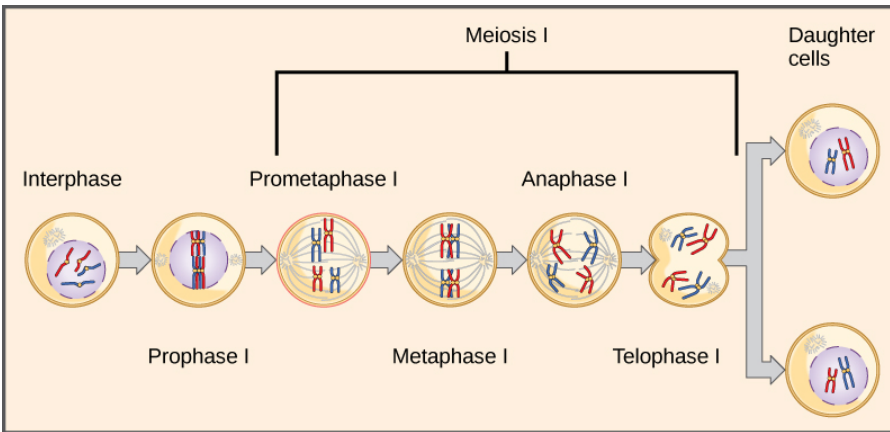
To demonstrate this with a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green seeds. The dominant seed color is yellow; therefore, the parental genotypes were YY for the plants with yellow seeds and yy for the plants with green seeds. A **Punnett square**, devised by the British geneticist Reginald Punnett, is useful for determining probabilities because it is drawn to predict all possible outcomes of all possible random fertilization events and their expected frequencies. [\[link\]](#) shows a Punnett square for a cross between a plant with yellow peas and one with green peas. To prepare a Punnett square, all possible combinations of the parental alleles (the genotypes of the gametes) are listed along the top (for one parent) and side (for the other parent) of a grid. The combinations of egg and sperm gametes are then made in the boxes in the table on the basis of which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant and recessive) is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible in the F₁ offspring. All offspring are Yy and have yellow seeds.

When the F₁ offspring are crossed with each other, each has an equal probability of contributing either a Y or a y to the F₂ offspring. The result is a 1 in 4 (25 percent) probability of both parents contributing a Y, resulting in an offspring with a yellow phenotype; a 25 percent probability of parent A contributing a Y and parent B a y, resulting in offspring with a yellow phenotype; a 25 percent probability of parent A contributing a y and parent B a Y, also resulting in a yellow phenotype; and a (25 percent) probability

of both parents contributing a y , resulting in a green phenotype. When counting all four possible outcomes, there is a 3 in 4 probability of offspring having the yellow phenotype and a 1 in 4 probability of offspring having the green phenotype. This explains why the results of Mendel's F_2 generation occurred in a 3:1 phenotypic ratio. Using large numbers of crosses, Mendel was able to calculate probabilities, found that they fit the model of inheritance, and use these to predict the outcomes of other crosses.

Law of Segregation

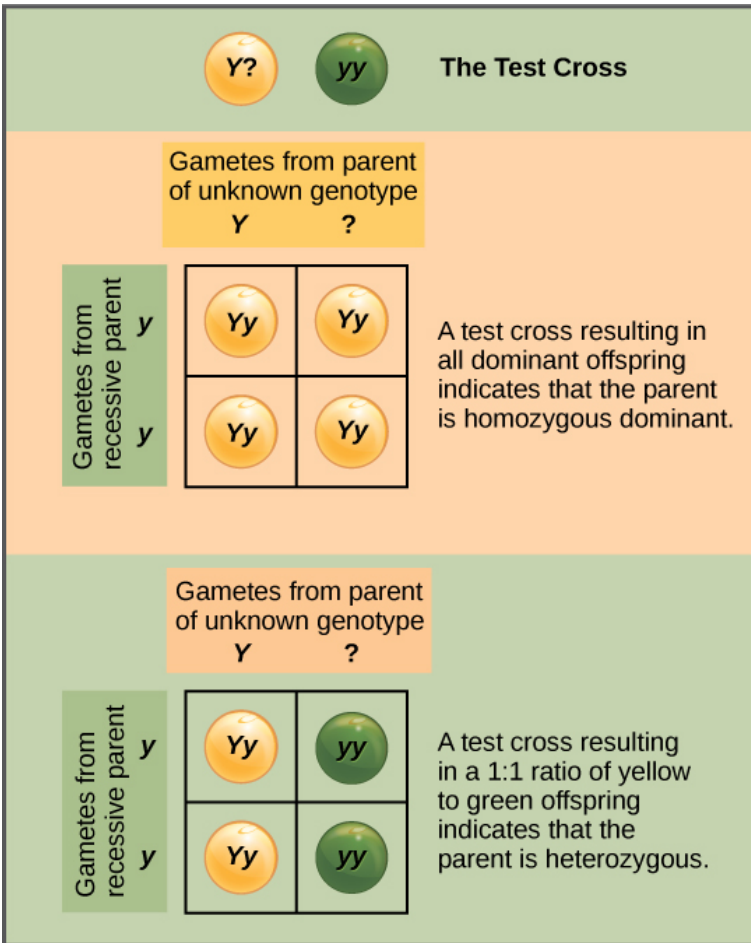
Observing that true-breeding pea plants with contrasting traits gave rise to F_1 generations that all expressed the dominant trait and F_2 generations that expressed the dominant and recessive traits in a 3:1 ratio, Mendel proposed the **law of segregation**. This law states that paired unit factors (genes) must segregate equally into gametes such that offspring have an equal likelihood of inheriting either factor. For the F_2 generation of a monohybrid cross, the following three possible combinations of genotypes result: homozygous dominant, heterozygous, or homozygous recessive. Because heterozygotes could arise from two different pathways (receiving one dominant and one recessive allele from either parent), and because heterozygotes and homozygous dominant individuals are phenotypically identical, the law supports Mendel's observed 3:1 phenotypic ratio. The equal segregation of alleles is the reason we can apply the Punnett square to accurately predict the offspring of parents with known genotypes. The physical basis of Mendel's law of segregation is the first division of meiosis in which the homologous chromosomes with their different versions of each gene are segregated into daughter nuclei. This process was not understood by the scientific community during Mendel's lifetime ([\[link\]](#)).



The first division in meiosis is shown.

Test Cross

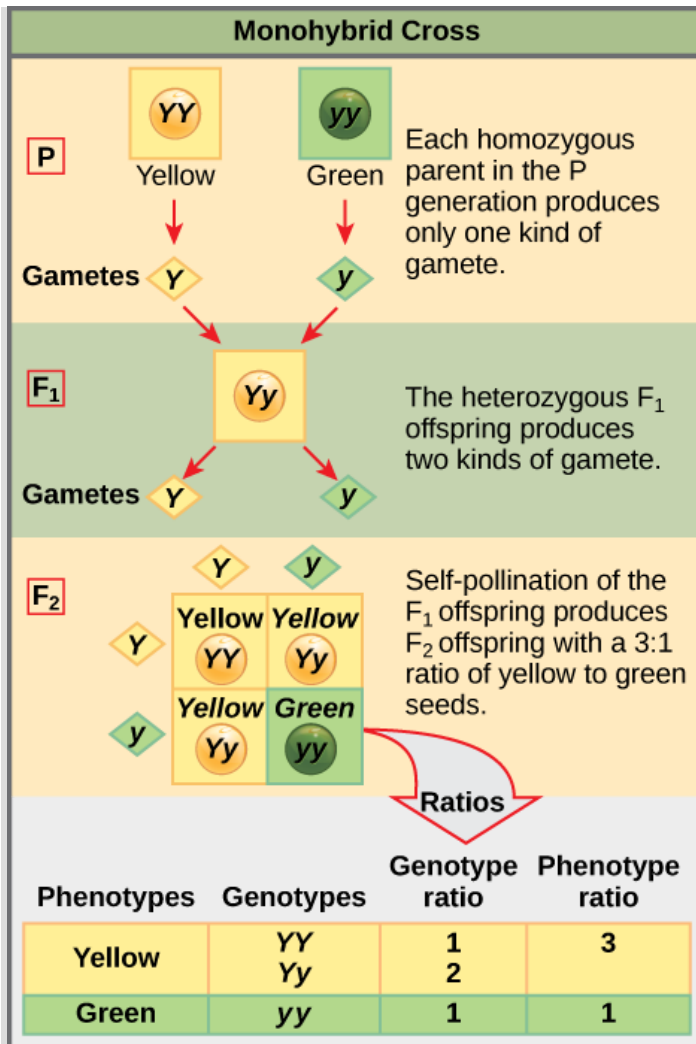
Beyond predicting the offspring of a cross between known homozygous or heterozygous parents, Mendel also developed a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote. Called the **test cross**, this technique is still used by plant and animal breeders. In a test cross, the dominant-expressing organism is crossed with an organism that is homozygous recessive for the same characteristic. If the dominant-expressing organism is a homozygote, then all F_1 offspring will be heterozygotes expressing the dominant trait ([\[link\]](#)). Alternatively, if the dominant-expressing organism is a heterozygote, the F_1 offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes ([\[link\]](#)). The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.



A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

Note:

Art Connection



This Punnett square shows the cross between plants with yellow seeds and green seeds. The cross between the true-breeding P plants produces F₁ heterozygotes that can be self-fertilized. The self-cross of the F₁ generation can be analyzed with a Punnett square to predict the genotypes of the F₂ generation. Given an inheritance pattern of dominant–recessive, the genotypic and phenotypic ratios can then be determined.

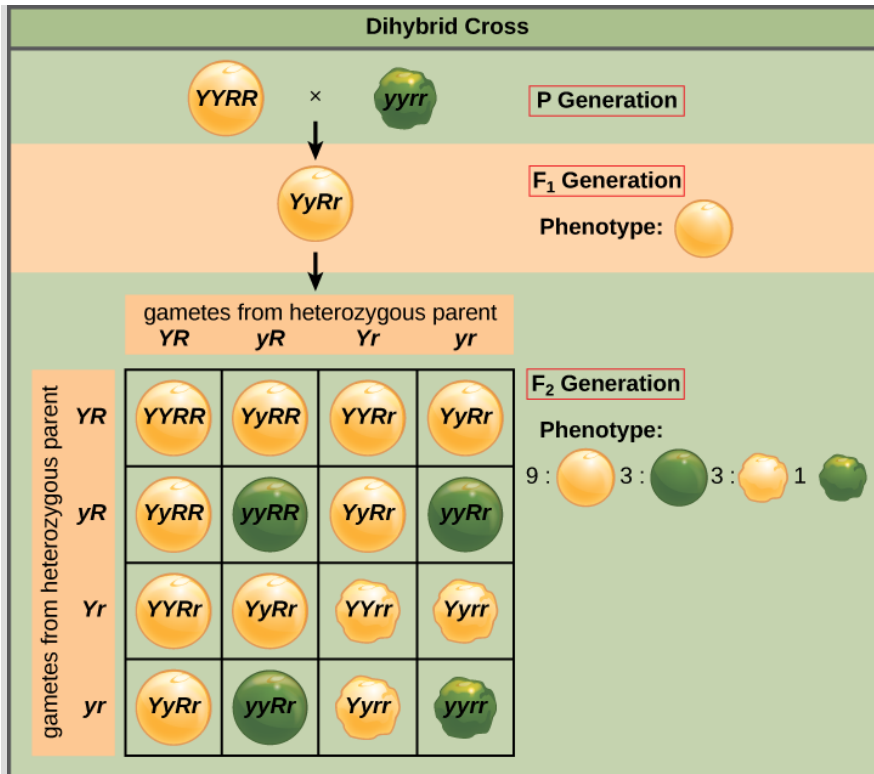
In pea plants, round peas (R) are dominant to wrinkled peas (r). You do a test cross between a pea plant with wrinkled peas (genotype rr) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

Law of Independent Assortment

Mendel's **law of independent assortment** states that genes do not influence each other with regard to the sorting of alleles into gametes, and every possible combination of alleles for every gene is equally likely to occur. Independent assortment of genes can be illustrated by the **dihybrid** cross, a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants, one that has wrinkled, green seeds ($rryy$) and another that has round, yellow seeds ($RRYY$). Because each parent is homozygous, the law of segregation indicates that the gametes for the wrinkled–green plant all are ry , and the gametes for the round–yellow plant are all RY . Therefore, the F_1 generation of offspring all are $RrYy$ ([link](#)).

Note:

Art Connection



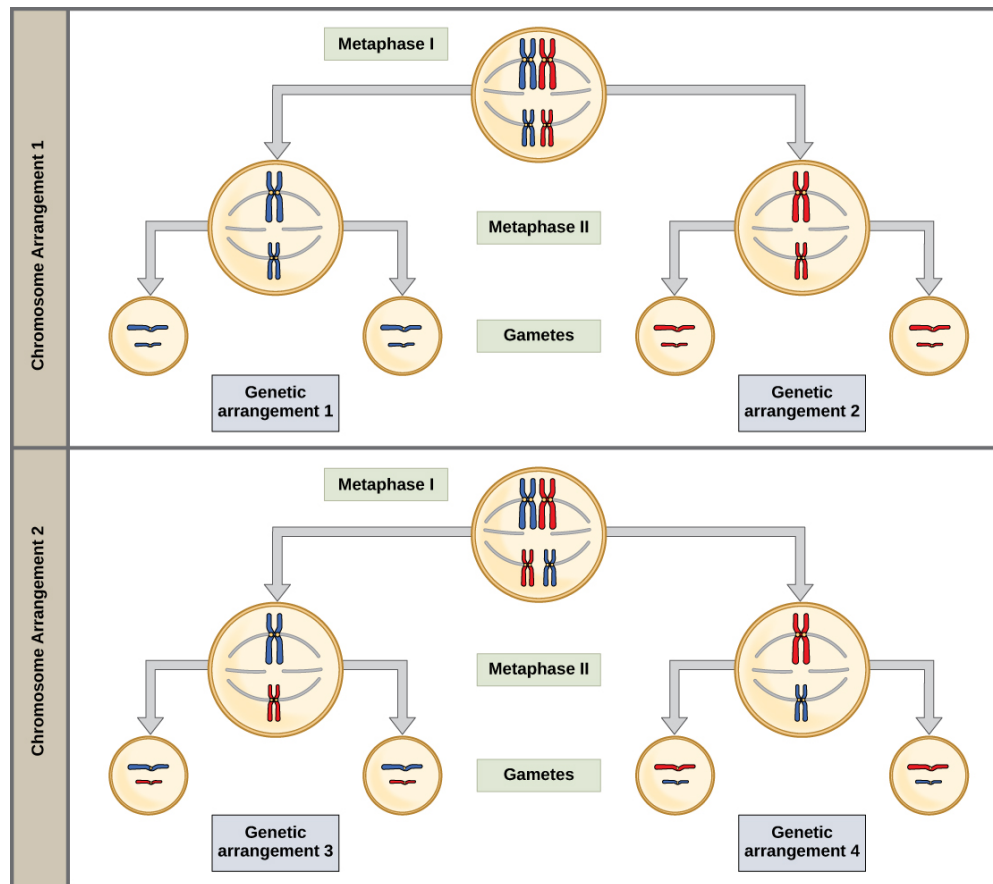
A dihybrid cross in pea plants involves the genes for seed color and texture. The P cross produces F₁ offspring that are all heterozygous for both characteristics. The resulting 9:3:3:1 F₂ phenotypic ratio is obtained using a Punnett square.

In pea plants, purple flowers (*P*) are dominant to white (*p*), and yellow peas (*Y*) are dominant to green (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

The gametes produced by the F₁ individuals must have one allele from each of the two genes. For example, a gamete could get an *R* allele for the seed shape gene and either a *Y* or a *y* allele for the seed color gene. It cannot get

both an *R* and an *r* allele; each gamete can have only one allele per gene. The law of independent assortment states that a gamete into which an *r* allele is sorted would be equally likely to contain either a *Y* or a *y* allele. Thus, there are four equally likely gametes that can be formed when the *RrYy* heterozygote is self-crossed, as follows: *RY*, *rY*, *Ry*, and *ry*. Arranging these gametes along the top and left of a 4×4 Punnett square ([\[link\]](#)) gives us 16 equally likely genotypic combinations. From these genotypes, we find a phenotypic ratio of 9 round–yellow:3 round–green:3 wrinkled–yellow:1 wrinkled–green ([\[link\]](#)). These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

The physical basis for the law of independent assortment also lies in meiosis I, in which the different homologous pairs line up in random orientations. Each gamete can contain any combination of paternal and maternal chromosomes (and therefore the genes on them) because the orientation of tetrads on the metaphase plane is random ([\[link\]](#)).



The random segregation into daughter nuclei that happens during the first division in meiosis can lead to a variety of possible genetic arrangements.

Section Summary

When true-breeding, or homozygous, individuals that differ for a certain trait are crossed, all of the offspring will be heterozygous for that trait. If the traits are inherited as dominant and recessive, the F_1 offspring will all exhibit the same phenotype as the parent homozygous for the dominant trait. If these heterozygous offspring are self-crossed, the resulting F_2 offspring will be equally likely to inherit gametes carrying the dominant or recessive trait, giving rise to offspring of which one quarter are homozygous dominant, half are heterozygous, and one quarter are

homozygous recessive. Because homozygous dominant and heterozygous individuals are phenotypically identical, the observed traits in the F_2 offspring will exhibit a ratio of three dominant to one recessive.

Mendel postulated that genes (characteristics) are inherited as pairs of alleles (traits) that behave in a dominant and recessive pattern. Alleles segregate into gametes such that each gamete is equally likely to receive either one of the two alleles present in a diploid individual. In addition, genes are assorted into gametes independently of one another. That is, in general, alleles are not more likely to segregate into a gamete with a particular allele of another gene.

Art Connections

Exercise:

Problem:

[\[link\]](#) In pea plants, round peas (R) are dominant to wrinkled peas (r). You do a test cross between a pea plant with wrinkled peas (genotype rr) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the parent plant is homozygous dominant or heterozygous?

Solution:

[\[link\]](#) You cannot be sure if the plant is homozygous or heterozygous as the data set is too small: by random chance, all three plants might have acquired only the dominant gene even if the recessive one is present.

Exercise:

Problem:

[\[link\]](#) In pea plants, purple flowers (*P*) are dominant to white (*p*), and yellow peas (*Y*) are dominant to green (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares would you need to complete a Punnett square analysis of this cross?

Solution:

[\[link\]](#) The possible genotypes are *PpYY*, *PpYy*, *ppYY*, and *ppYy*. The former two genotypes would result in plants with purple flowers and yellow peas, while the latter two genotypes would result in plants with white flowers with yellow peas, for a 1:1 ratio of each phenotype. You only need a 2×2 Punnett square (four squares total) to do this analysis because two of the alleles are homozygous.

Multiple Choice

Exercise:**Problem:**

The observable traits expressed by an organism are described as its _____.

- a. phenotype
- b. genotype
- c. alleles
- d. zygote

Solution:

A

Exercise:

Problem:

A recessive trait will be observed in individuals that are _____ for that trait.

- a. heterozygous
- b. homozygous or heterozygous
- c. homozygous
- d. diploid

Solution:

C

Exercise:**Problem:**

What are the types of gametes that can be produced by an individual with the genotype $AaBb$?

- a. Aa, Bb
- b. AA, aa, BB, bb
- c. AB, Ab, aB, ab
- d. AB, ab

Solution:

C

Exercise:

Problem: What is the reason for doing a test cross?

- a. to identify heterozygous individuals with the dominant phenotype
- b. to determine which allele is dominant and which is recessive
- c. to identify homozygous recessive individuals in the F_2

d. to determine if two genes assort independently

Solution:

A

Free Response

Exercise:

Problem:

Use a Punnett square to predict the offspring in a cross between a dwarf pea plant (homozygous recessive) and a tall pea plant (heterozygous). What is the phenotypic ratio of the offspring?

Solution:

The Punnett square would be 2×2 and will have T and T along the top and T and t along the left side. Clockwise from the top left, the genotypes listed within the boxes will be Tt , Tt , tt , and tt . The phenotypic ratio will be 1 tall:1 dwarf.

Exercise:

Problem:

Use a Punnett square to predict the offspring in a cross between a tall pea plant (heterozygous) and a tall pea plant (heterozygous). What is the genotypic ratio of the offspring?

Solution:

The Punnett square will be 2×2 and will have T and t along the top and T and t along the left side. Clockwise from the top left, the genotypes listed within the boxes will be TT , Tt , Tt , and tt . The genotypic ratio will be $1TT:2Tt:1tt$.

Glossary

allele

one of two or more variants of a gene that determines a particular trait for a characteristic

dihybrid

the result of a cross between two true-breeding parents that express different traits for two characteristics

genotype

the underlying genetic makeup, consisting of both physically visible and non-expressed alleles, of an organism

heterozygous

having two different alleles for a given gene on the homologous chromosomes

homozygous

having two identical alleles for a given gene on the homologous chromosomes

law of dominance

in a heterozygote, one trait will conceal the presence of another trait for the same characteristic

law of independent assortment

genes do not influence each other with regard to sorting of alleles into gametes; every possible combination of alleles is equally likely to occur

law of segregation

paired unit factors (i.e., genes) segregate equally into gametes such that offspring have an equal likelihood of inheriting any combination of factors

monohybrid

the result of a cross between two true-breeding parents that express different traits for only one characteristic

phenotype

the observable traits expressed by an organism

Punnett square

a visual representation of a cross between two individuals in which the gametes of each individual are denoted along the top and side of a grid, respectively, and the possible zygotic genotypes are recombined at each box in the grid

test cross

a cross between a dominant expressing individual with an unknown genotype and a homozygous recessive individual; the offspring phenotypes indicate whether the unknown parent is heterozygous or homozygous for the dominant trait

Extensions of the Laws of Inheritance

By the end of this section, you will be able to:

- Identify non-Mendelian inheritance patterns such as incomplete dominance, codominance, multiple alleles, and sex linkage from the results of crosses
- Explain the effect of linkage and recombination on gamete genotypes
- Explain the phenotypic outcomes of epistatic effects among genes

Mendel studied traits with only one mode of inheritance in pea plants. The inheritance of the traits he studied all followed the relatively simple pattern of dominant and recessive alleles for a single characteristic. There are several important modes of inheritance, discovered after Mendel's work, that do not follow the dominant and recessive, single-gene model.

Alternatives to Dominance and Recessiveness

Mendel's experiments with pea plants suggested that: 1) two types of "units" or alleles exist for every gene; 2) alleles maintain their integrity in each generation (no blending); and 3) in the presence of the dominant allele, the recessive allele is hidden, with no contribution to the phenotype. Therefore, recessive alleles can be "carried" and not expressed by individuals. Such heterozygous individuals are sometimes referred to as "carriers." Since then, genetic studies in other organisms have shown that much more complexity exists, but that the fundamental principles of Mendelian genetics still hold true. In the sections to follow, we consider some of the extensions of Mendelism.

Incomplete Dominance

Mendel's results, demonstrating that traits are inherited as dominant and recessive pairs, contradicted the view at that time that offspring exhibited a blend of their parents' traits. However, the heterozygote phenotype occasionally does appear to be intermediate between the two parents. For example, in the snapdragon, *Antirrhinum majus* ([\[link\]](#)), a cross between a homozygous parent with white flowers ($C^W C^W$) and a homozygous parent

with red flowers ($C^R C^R$) will produce offspring with pink flowers ($C^R C^W$). (Note that different genotypic abbreviations are used for Mendelian extensions to distinguish these patterns from simple dominance and recessiveness.) This pattern of inheritance is described as **incomplete dominance**, meaning that one of the alleles appears in the phenotype in the heterozygote, but not to the exclusion of the other, which can also be seen. The allele for red flowers is incompletely dominant over the allele for white flowers. However, the results of a heterozygote self-cross can still be predicted, just as with Mendelian dominant and recessive crosses. In this case, the genotypic ratio would be 1 $C^R C^R$:2 $C^R C^W$:1 $C^W C^W$, and the phenotypic ratio would be 1:2:1 for red:pink:white. The basis for the intermediate color in the heterozygote is simply that the pigment produced by the red allele (anthocyanin) is diluted in the heterozygote and therefore appears pink because of the white background of the flower petals.



These pink flowers of a heterozygote snapdragon result from incomplete

dominance. (credit:
"storebukkebruse"/Flickr)

Codominance

A variation on incomplete dominance is **codominance**, in which both alleles for the same characteristic are simultaneously expressed in the heterozygote. An example of codominance occurs in the ABO blood groups of humans. The A and B alleles are expressed in the form of A or B molecules present on the surface of red blood cells. Homozygotes ($I^A I^A$ and $I^B I^B$) express either the A or the B phenotype, and heterozygotes ($I^A I^B$) express both phenotypes equally. The $I^A I^B$ individual has blood type AB. In a self-cross between heterozygotes expressing a codominant trait, the three possible offspring genotypes are phenotypically distinct. However, the 1:2:1 genotypic ratio characteristic of a Mendelian monohybrid cross still applies ([link](#)).

Codominant Cross			
	I^A	I^B	
I^A	$I^A I^A$ A	$I^A I^B$ AB	
I^B	$I^A I^B$ AB	$I^B I^B$ B	
			Ratios
Genotypes		Genotype ratio	
AA		1	
AB		2	
BB		1	

This Punnet square shows an AB/AB blood type cross

Multiple Alleles

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. We now know that this is an oversimplification. Although individual humans (and all diploid organisms) can only have two alleles for a given gene, multiple alleles may exist at the population level, such that many combinations of two alleles are observed. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype in the natural population as the **wild type** (often abbreviated “+”). All other phenotypes or genotypes are considered variants (mutants) of this typical form, meaning they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele.

An example of multiple alleles is the ABO blood-type system in humans. In this case, there are three alleles circulating in the population. The I^A allele codes for A molecules on the red blood cells, the I^B allele codes for B molecules on the surface of red blood cells, and the i allele codes for no molecules on the red blood cells. In this case, the I^A and I^B alleles are codominant with each other and are both dominant over the i allele. Although there are three alleles present in a population, each individual only gets two of the alleles from their parents. This produces the genotypes and phenotypes shown in [\[link\]](#). Notice that instead of three genotypes, there are six different genotypes when there are three alleles. The number of possible phenotypes depends on the dominance relationships between the three alleles.

Inheritance of the ABO Blood System in Humans			
	I^A	I^B	i
I^A	$I^A I^A$ A	$I^A I^B$ AB	$I^A i$ A
I^B	$I^B I^A$ AB	$I^B I^B$ B	$I^B i$ B
i	$i I^A$ A	$i I^B$ B	$i i$ O

Inheritance of the ABO blood system in humans is shown.

Note:
Evolution in Action

Multiple Alleles Confer Drug Resistance in the Malaria Parasite

Malaria is a parasitic disease in humans that is transmitted by infected female mosquitoes, including *Anopheles gambiae*, and is characterized by cyclic high fevers, chills, flu-like symptoms, and severe anemia.

Plasmodium falciparum and *P. vivax* are the most common causative agents of malaria, and *P. falciparum* is the most deadly. When promptly and correctly treated, *P. falciparum* malaria has a mortality rate of 0.1 percent. However, in some parts of the world, the parasite has evolved resistance to commonly used malaria treatments, so the most effective malarial treatments can vary by geographic region.

In Southeast Asia, Africa, and South America, *P. falciparum* has developed resistance to the anti-malarial drugs chloroquine, mefloquine, and sulfadoxine-pyrimethamine. *P. falciparum*, which is haploid during the life stage in which it is infective to humans, has evolved multiple drug-resistant mutant alleles of the *dhps* gene. Varying degrees of sulfadoxine resistance are associated with each of these alleles. Being haploid, *P. falciparum* needs only one drug-resistant allele to express this trait.

In Southeast Asia, different sulfadoxine-resistant alleles of the *dhps* gene are localized to different geographic regions. This is a common evolutionary phenomenon that comes about because drug-resistant mutants arise in a population and interbreed with other *P. falciparum* isolates in close proximity. Sulfadoxine-resistant parasites cause considerable human hardship in regions in which this drug is widely used as an over-the-counter malaria remedy. As is common with pathogens that multiply to large numbers within an infection cycle, *P. falciparum* evolves relatively rapidly (over a decade or so) in response to the selective pressure of commonly used anti-malarial drugs. For this reason, scientists must constantly work to develop new drugs or drug combinations to combat the worldwide malaria burden. [\[footnote\]](#)

Sumiti Vinayak et al., “Origin and Evolution of Sulfadoxine Resistant *Plasmodium falciparum*,” *PLoS Pathogens* 6 (2010): e1000830.

Sex-Linked Traits

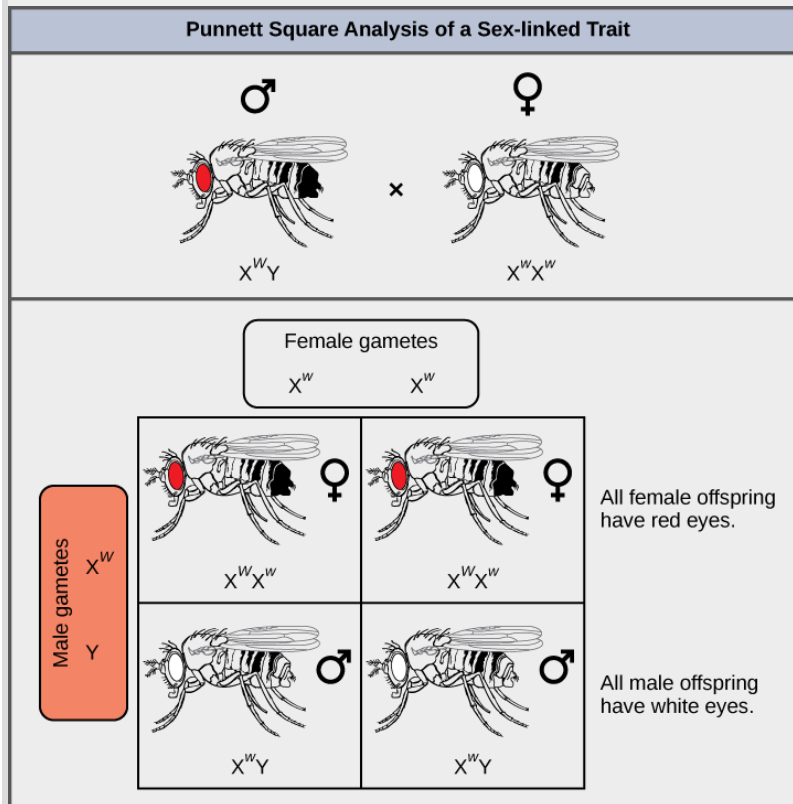
In humans, as well as in many other animals and some plants, the sex of the individual is determined by sex chromosomes—one pair of non-homologous chromosomes. Until now, we have only considered inheritance patterns among non-sex chromosomes, or autosomes. In addition to 22 homologous pairs of autosomes, human females have a homologous pair of X chromosomes, whereas human males have an XY chromosome pair. Although the Y chromosome contains a small region of similarity to the X chromosome so that they can pair during meiosis, the Y chromosome is much shorter and contains fewer genes. When a gene being examined is present on the X, but not the Y, chromosome, it is **X-linked**.

Eye color in *Drosophila*, the common fruit fly, was the first X-linked trait to be identified. Thomas Hunt Morgan mapped this trait to the X chromosome in 1910. Like humans, *Drosophila* males have an XY chromosome pair, and females are XX. In flies the wild-type eye color is red (X^W) and is dominant to white eye color (X^w) ([link](#)). Because of the location of the eye-color gene, reciprocal crosses do not produce the same offspring ratios. Males are said to be **hemizygous**, in that they have only one allele for any X-linked characteristic. Hemizyosity makes descriptions of dominance and recessiveness irrelevant for XY males. *Drosophila* males lack the white gene on the Y chromosome; that is, their genotype can only be X^WY or X^wY . In contrast, females have two allele copies of this gene and can be X^WX^W , X^WX^w , or X^wX^w .



In *Drosophila*, the gene for eye color is located on the X chromosome. Red eye color is wild-type and is dominant to white eye color.

In an X-linked cross, the genotypes of F_1 and F_2 offspring depend on whether the recessive trait was expressed by the male or the female in the P generation. With respect to *Drosophila* eye color, when the P male expresses the white-eye phenotype and the female is homozygously red-eyed, all members of the F_1 generation exhibit red eyes ([link](#)). The F_1 females are heterozygous ($X^W X^w$), and the males are all $X^W Y$, having received their X chromosome from the homozygous dominant P female and their Y chromosome from the P male. A subsequent cross between the $X^W X^w$ female and the $X^W Y$ male would produce only red-eyed females (with $X^W X^W$ or $X^W X^w$ genotypes) and both red- and white-eyed males (with $X^W Y$ or $X^w Y$ genotypes). Now, consider a cross between a homozygous white-eyed female and a male with red eyes. The F_1 generation would exhibit only heterozygous red-eyed females ($X^W X^w$) and only white-eyed males ($X^w Y$). Half of the F_2 females would be red-eyed ($X^W X^W$) and half would be white-eyed ($X^w X^w$). Similarly, half of the F_2 males would be red-eyed ($X^W Y$) and half would be white-eyed ($X^w Y$).

Note:**Art Connection**

Crosses involving sex-linked traits often give rise to different phenotypes for the different sexes of offspring, as is the case for this cross involving red and white eye color in *Drosophila*. In the diagram, w is the white-eye mutant allele and W is the wild-type, red-eye allele.

What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

Discoveries in fruit fly genetics can be applied to human genetics. When a female parent is homozygous for a recessive X-linked trait, she will pass the

trait on to 100 percent of her male offspring, because the males will receive the Y chromosome from the male parent. In humans, the alleles for certain conditions (some color-blindness, hemophilia, and muscular dystrophy) are X-linked. Females who are heterozygous for these diseases are said to be carriers and may not exhibit any phenotypic effects. These females will pass the disease to half of their sons and will pass carrier status to half of their daughters; therefore, X-linked traits appear more frequently in males than females.

In some groups of organisms with sex chromosomes, the sex with the non-homologous sex chromosomes is the female rather than the male. This is the case for all birds. In this case, sex-linked traits will be more likely to appear in the female, in whom they are hemizygous.

Note:

Concept in Action



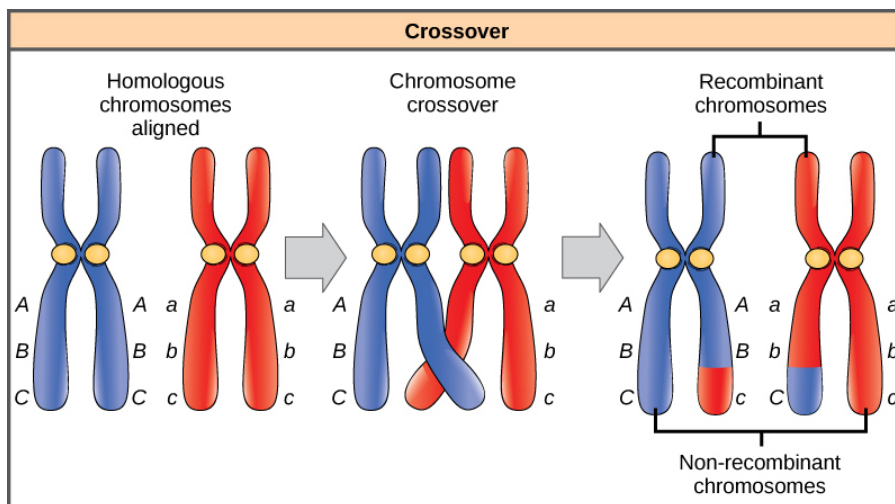
Watch [this video](#) to learn more about sex-linked traits.

Linked Genes Violate the Law of Independent Assortment

Although all of Mendel's pea plant characteristics behaved according to the law of independent assortment, we now know that some allele combinations are not inherited independently of each other. Genes that are located on separate, non-homologous chromosomes will always sort independently. However, each chromosome contains hundreds or thousands of genes, organized linearly on chromosomes like beads on a string. The segregation of alleles into gametes can be influenced by **linkage**, in which genes that

are located physically close to each other on the same chromosome are more likely to be inherited as a pair. However, because of the process of recombination, or “crossover,” it is possible for two genes on the same chromosome to behave independently, or as if they are not linked. To understand this, let us consider the biological basis of gene linkage and recombination.

Homologous chromosomes possess the same genes in the same order, though the specific alleles of the gene can be different on each of the two chromosomes. Recall that during interphase and prophase I of meiosis, homologous chromosomes first replicate and then synapse, with like genes on the homologs aligning with each other. At this stage, segments of homologous chromosomes exchange linear segments of genetic material ([link]). This process is called **recombination**, or crossover, and it is a common genetic process. Because the genes are aligned during recombination, the gene order is not altered. Instead, the result of recombination is that maternal and paternal alleles are combined onto the same chromosome. Across a given chromosome, several recombination events may occur, causing extensive shuffling of alleles.



The process of crossover, or recombination, occurs when two homologous chromosomes align and exchange a segment of genetic material.

When two genes are located on the same chromosome, they are considered linked, and their alleles tend to be transmitted through meiosis together. To exemplify this, imagine a dihybrid cross involving flower color and plant height in which the genes are next to each other on the chromosome. If one homologous chromosome has alleles for tall plants and red flowers, and the other chromosome has genes for short plants and yellow flowers, then when the gametes are formed, the tall and red alleles will tend to go together into a gamete and the short and yellow alleles will go into other gametes. These are called the parental genotypes because they have been inherited intact from the parents of the individual producing gametes. But unlike if the genes were on different chromosomes, there will be no gametes with tall and yellow alleles and no gametes with short and red alleles. If you create a Punnett square with these gametes, you will see that the classical Mendelian prediction of a 9:3:3:1 outcome of a dihybrid cross would not apply. As the distance between two genes increases, the probability of one or more crossovers between them increases and the genes behave more like they are on separate chromosomes. Geneticists have used the proportion of recombinant gametes (the ones not like the parents) as a measure of how far apart genes are on a chromosome. Using this information, they have constructed linkage maps of genes on chromosomes for well-studied organisms, including humans.

Mendel's seminal publication makes no mention of linkage, and many researchers have questioned whether he encountered linkage but chose not to publish those crosses out of concern that they would invalidate his independent assortment postulate. The garden pea has seven chromosomes, and some have suggested that his choice of seven characteristics was not a coincidence. However, even if the genes he examined were not located on separate chromosomes, it is possible that he simply did not observe linkage because of the extensive shuffling effects of recombination.

Epistasis

Mendel's studies in pea plants implied that the sum of an individual's phenotype was controlled by genes (or as he called them, unit factors), such

that every characteristic was distinctly and completely controlled by a single gene. In fact, single observable characteristics are almost always under the influence of multiple genes (each with two or more alleles) acting in unison. For example, at least eight genes contribute to eye color in humans.

Note:

Concept in Action



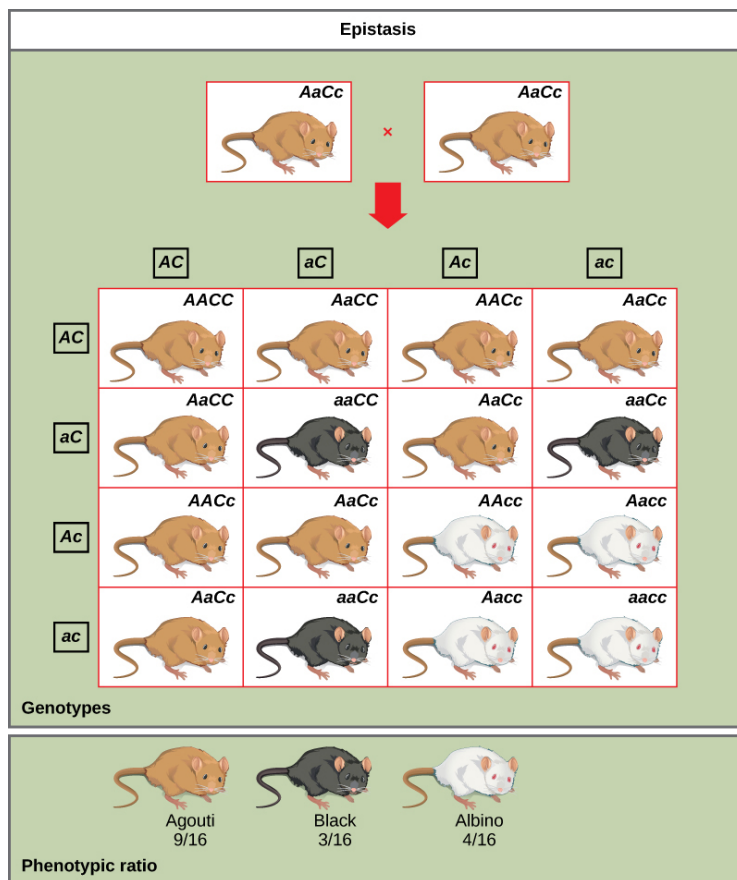
Eye color in humans is determined by multiple alleles. Use the [Eye Color Calculator](#) to predict the eye color of children from parental eye color.

In some cases, several genes can contribute to aspects of a common phenotype without their gene products ever directly interacting. In the case of organ development, for instance, genes may be expressed sequentially, with each gene adding to the complexity and specificity of the organ. Genes may function in complementary or synergistic fashions, such that two or more genes expressed simultaneously affect a phenotype. An apparent example of this occurs with human skin color, which appears to involve the action of at least three (and probably more) genes. Cases in which inheritance for a characteristic like skin color or human height depend on the combined effects of numerous genes are called polygenic inheritance.

Genes may also oppose each other, with one gene suppressing the expression of another. In **epistasis**, the interaction between genes is antagonistic, such that one gene masks or interferes with the expression of another. “Epistasis” is a word composed of Greek roots meaning “standing upon.” The alleles that are being masked or silenced are said to be

hypostatic to the epistatic alleles that are doing the masking. Often the biochemical basis of epistasis is a gene pathway in which expression of one gene is dependent on the function of a gene that precedes or follows it in the pathway.

An example of epistasis is pigmentation in mice. The wild-type coat color, agouti (AA) is dominant to solid-colored fur (aa). However, a separate gene C, when present as the recessive homozygote (cc), negates any expression of pigment from the A gene and results in an albino mouse ([link](#)). Therefore, the genotypes *AAcc*, *Aacc*, and *aacc* all produce the same albino phenotype. A cross between heterozygotes for both genes (*AaCc* x *AaCc*) would generate offspring with a phenotypic ratio of 9 agouti:3 black:4 albino ([link](#)). In this case, the C gene is epistatic to the A gene.



In this example of epistasis, one gene

(C) masks the expression of another (A) for coat color. When the C allele is present, coat color is expressed; when it is absent (cc), no coat color is expressed. Coat color depends on the A gene, which shows dominance, with the recessive homozygote showing a different phenotype than the heterozygote or dominant homozygote.

Section Summary

Alleles do not always behave in dominant and recessive patterns. Incomplete dominance describes situations in which the heterozygote exhibits a phenotype that is intermediate between the homozygous phenotypes. Codominance describes the simultaneous expression of both of the alleles in the heterozygote. Although diploid organisms can only have two alleles for any given gene, it is common for more than two alleles for a gene to exist in a population. In humans, as in many animals and some plants, females have two X chromosomes and males have one X and one Y chromosome. Genes that are present on the X but not the Y chromosome are said to be X-linked, such that males only inherit one allele for the gene, and females inherit two.

According to Mendel's law of independent assortment, genes sort independently of each other into gametes during meiosis. This occurs because chromosomes, on which the genes reside, assort independently during meiosis and crossovers cause most genes on the same chromosomes to also behave independently. When genes are located in close proximity on the same chromosome, their alleles tend to be inherited together. This results in offspring ratios that violate Mendel's law of independent assortment. However, recombination serves to exchange genetic material on homologous chromosomes such that maternal and paternal alleles may be recombined on the same chromosome. This is why alleles on a given chromosome are not always inherited together. Recombination is a random

event occurring anywhere on a chromosome. Therefore, genes that are far apart on the same chromosome are likely to still assort independently because of recombination events that occurred in the intervening chromosomal space.

Whether or not they are sorting independently, genes may interact at the level of gene products, such that the expression of an allele for one gene masks or modifies the expression of an allele for a different gene. This is called epistasis.

Art Connections

Exercise:

Problem:

[\[link\]](#) What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

Solution:

[\[link\]](#) Half of the female offspring would be heterozygous ($X^W X^w$) with red eyes, and half would be homozygous recessive ($X^w X^w$) with white eyes. Half of the male offspring would be hemizygous dominant ($X^W Y$) with red eyes, and half would be hemizygous recessive ($X^w Y$) with white eyes.

Multiple Choice

Exercise:

Problem:

If black and white true-breeding mice are mated and the result is all gray offspring, what inheritance pattern would this be indicative of?

- a. dominance
- b. codominance

- c. multiple alleles
 - d. incomplete dominance
-

Solution:

D

Exercise:

Problem:

The ABO blood groups in humans are expressed as the I^A , I^B , and i alleles. The I^A allele encodes the A blood group antigen, I^B encodes B, and i encodes O. Both A and B are dominant to O. If a heterozygous blood type A parent ($I^A i$) and a heterozygous blood type B parent ($I^B i$) mate, one quarter of their offspring are expected to have the AB blood type ($I^A I^B$) in which both antigens are expressed equally. Therefore, ABO blood groups are an example of:

- a. multiple alleles and incomplete dominance
 - b. codominance and incomplete dominance
 - c. incomplete dominance only
 - d. multiple alleles and codominance
-

Solution:

D

Exercise:

Problem:

In a cross between a homozygous red-eyed female fruit fly and a white-eyed male fruit fly, what is the expected outcome?

- a. all white-eyed male offspring
- b. all white-eyed female offspring
- c. all red-eyed offspring

d. half white-eyed make offspring

Solution:

C

Exercise:

Problem:

When a population has a gene with four alleles circulating, how many possible genotypes are there?

- a. 3
- b. 6
- c. 10
- d. 16

Solution:

C

Free Response

Exercise:

Problem: Can a male be a carrier of red-green color blindness?

Solution:

No, males can only express color blindness and cannot carry it because an individual needs two X chromosomes to be a carrier.

Exercise:

Problem:

Could an individual with blood type O (genotype ii) be a legitimate child of parents in which one parent had blood type A and the other parent had blood type B?

Solution:

Yes this child could have come from these parents. The child would have inherited an i allele from each parent and for this to happen the type A parent had to have genotype $I^A i$ and the type b parent had to have genotype $I^B i$.

Glossary

codominance

in a heterozygote, complete and simultaneous expression of both alleles for the same characteristic

epistasis

an interaction between genes such that one gene masks or interferes with the expression of another

hemizygous

the presence of only one allele for a characteristic, as in X-linkage; hemizyosity makes descriptions of dominance and recessiveness irrelevant

incomplete dominance

in a heterozygote, expression of two contrasting alleles such that the individual displays an intermediate phenotype

linkage

a phenomenon in which alleles that are located in close proximity to each other on the same chromosome are more likely to be inherited together

recombination

the process during meiosis in which homologous chromosomes exchange linear segments of genetic material, thereby dramatically increasing genetic variation in the offspring and separating linked genes

wild type

the most commonly occurring genotype or phenotype for a given characteristic found in a population

X-linked

a gene present on the X chromosome, but not the Y chromosome

Introduction

class="introduction"

The diversity
of life on
Earth is the
result of
evolution, a
continuous
process that
is still
occurring.

(credit
“wolf”:
modification
of work by

Gary
Kramer,
USFWS;

credit
“coral”:
modification
of work by
William
Harrigan,
NOAA;

credit
“river”:
modification
of work by
Vojtěch
Dostál;

credit
“protozoa”:
modification
of work by
Sharon

Franklin,
Stephen
Ausmus,
USDA ARS;
credit “fish”
modification
of work by
Christian
Mehlführer;
credit
“mushroom”
, “bee”:
modification
of work by
Cory Zanker;
credit “tree”:
modification
of work by
Joseph
Kranak)



All species of living organisms—from the bacteria on our skin, to the trees in our yards, to the birds outside—evolved at some point from a different species. Although it may seem that living things today stay much the same from generation to generation, that is not the case: evolution is ongoing. Evolution is the process through which the characteristics of species change and through which new species arise.

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. Its power is that it provides direction for predictions about living things that are borne out in experiment after experiment. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote that “nothing makes sense in biology except in the light of evolution.”^[footnote] He meant that the principle that all life has evolved and diversified from a common ancestor is the foundation from which we understand all other questions in biology. This chapter will explain some of the mechanisms for evolutionary change and the kinds of questions that biologists can and have answered using evolutionary theory.

Theodosius Dobzhansky. "Biology, Molecular and Organismic." *American Zoologist* 4, no. 4 (1964): 449.

Discovering How Populations Change

By the end of this section, you will be able to:

- Explain how Darwin's theory of evolution differed from the current view at the time
- Describe how the present-day theory of evolution was developed
- Describe how population genetics is used to study the evolution of populations

The theory of evolution by natural selection describes a mechanism for species change over time. That species change had been suggested and debated well before Darwin. The view that species were static and unchanging was grounded in the writings of Plato, yet there were also ancient Greeks that expressed evolutionary ideas.

In the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc, Comte de Buffon and even by Charles Darwin's grandfather, Erasmus Darwin. During this time, it was also accepted that there were extinct species. At the same time, James Hutton, the Scottish naturalist, proposed that geological change occurred gradually by the accumulation of small changes from processes (over long periods of time) just like those happening today. This contrasted with the predominant view that the geology of the planet was a consequence of catastrophic events occurring during a relatively brief past. Hutton's view was later popularized by the geologist Charles Lyell in the nineteenth century. Lyell became a friend to Darwin and his ideas were very influential on Darwin's thinking. Lyell argued that the greater age of Earth gave more time for gradual change in species, and the process provided an analogy for gradual change in species.

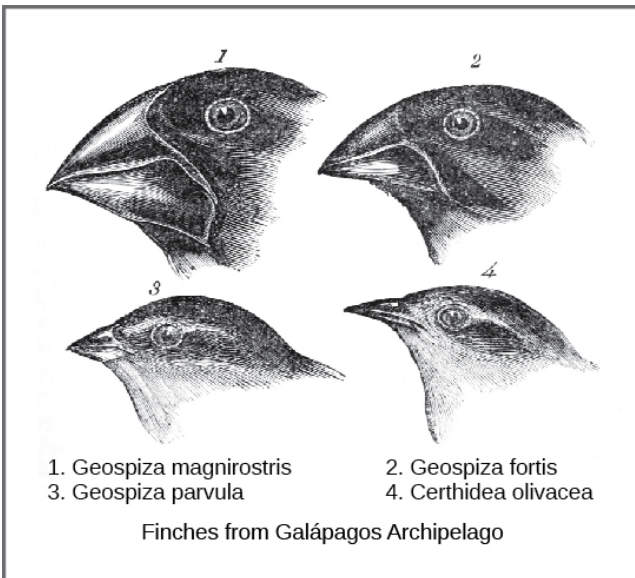
In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a mechanism for evolutionary change that is now referred to as **inheritance of acquired characteristics**. In Lamarck's theory, modifications in an individual caused by its environment, or the use or disuse of a structure during its lifetime, could be inherited by its offspring and, thus, bring about change in a species. While this mechanism for evolutionary change as described by Lamarck was discredited, Lamarck's ideas were an important influence on evolutionary thought. The inscription

on the statue of Lamarck that stands at the gates of the Jardin des Plantes in Paris describes him as the “founder of the doctrine of evolution.”

Charles Darwin and Natural Selection

The actual mechanism for evolution was independently conceived of and described by two naturalists, Charles Darwin and Alfred Russell Wallace, in the mid-nineteenth century. Importantly, each spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world on *H.M.S. Beagle*, visiting South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin’s journey, like Wallace’s later journeys in the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands (west of Ecuador). On these islands, Darwin observed species of organisms on different islands that were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species that each had a unique beak shape ([\[link\]](#)). He observed both that these finches closely resembled another finch species on the mainland of South America and that the group of species in the Galápagos formed a graded series of beak sizes and shapes, with very small differences between the most similar. Darwin imagined that the island species might be all species modified from one original mainland species. In 1860, he wrote, “Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends.”[\[footnote\]](#)

Charles Darwin, *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle Round the World, under the Command of Capt. Fitz Roy, R.N.*, 2nd. ed. (London: John Murray, 1860), <http://www.archive.org/details/journalofresea00darw>.

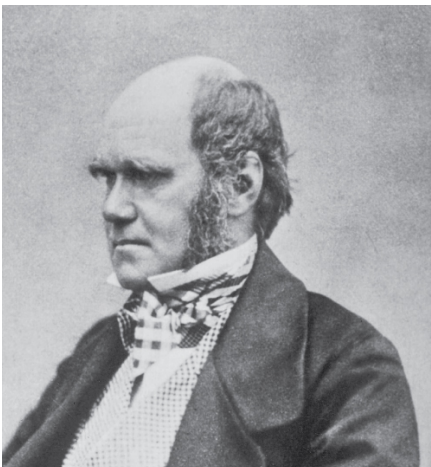


Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources. This illustration shows the beak shapes for four species of ground finch: 1. *Geospiza magnirostris* (the large ground finch), 2. *G. fortis* (the medium ground finch), 3. *G. parvula* (the small tree finch), and 4. *Certhidea olivacea* (the green-warbler finch).

Wallace and Darwin both observed similar patterns in other organisms and independently conceived a mechanism to explain how and why such changes could take place. Darwin called this mechanism natural selection. **Natural selection**, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, the characteristics of organisms are inherited, or passed from parent to offspring. Second, more offspring are

produced than are able to survive; in other words, resources for survival and reproduction are limited. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is a competition for those resources in each generation. Both Darwin and Wallace's understanding of this principle came from reading an essay by the economist Thomas Malthus, who discussed this principle in relation to human populations. Third, offspring vary among each other in regard to their characteristics and those variations are inherited. Out of these three principles, Darwin and Wallace reasoned that offspring with inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over generations in a process that Darwin called "descent with modification."

Papers by Darwin and Wallace ([\[link\]](#)) presenting the idea of natural selection were read together in 1858 before the Linnaean Society in London. The following year Darwin's book, *On the Origin of Species*, was published, which outlined in considerable detail his arguments for evolution by natural selection.



(a)

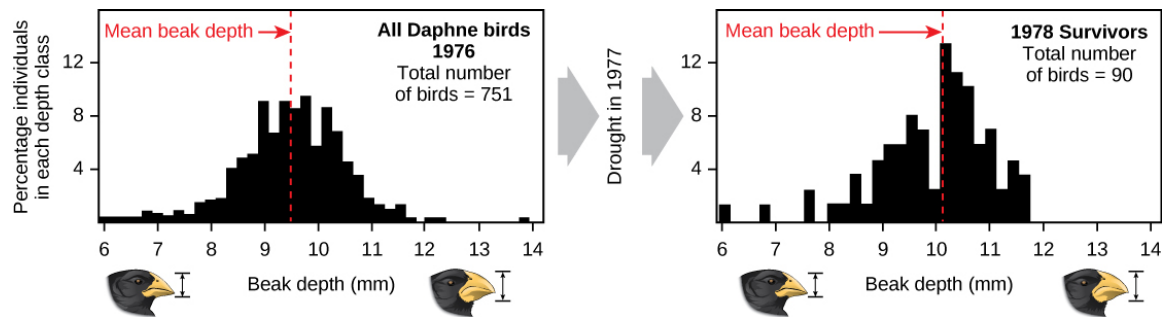


(b)

(a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that

were presented together before the Linnean Society in 1858.

Demonstrations of evolution by natural selection can be time consuming. One of the best demonstrations has been in the very birds that helped to inspire the theory, the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major. The medium ground finch feeds on seeds. The birds have inherited variation in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller billed birds feed more efficiently on small, soft seeds. During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically: the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year. The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger ([\[link\]](#)). This was clear evidence for natural selection (differences in survival) of bill size caused by the availability of seeds. The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection on and evolution of bill size in this species in response to changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.



A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

Variation and Adaptation

Natural selection can only take place if there is **variation**, or differences, among individuals in a population. Importantly, these differences must have some genetic basis; otherwise, selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual being taller because of better nutrition rather than different genes.

Genetic diversity in a population comes from two main sources: mutation and sexual reproduction. Mutation, a change in DNA, is the ultimate source of new alleles or new genetic variation in any population. An individual that has a mutated gene might have a different trait than other individuals in the population. However, this is not always the case. A mutation can have one of three outcomes on the organisms' appearance (or phenotype):

- A mutation may affect the phenotype of the organism in a way that gives it reduced fitness—lower likelihood of survival, resulting in fewer offspring.
- A mutation may produce a phenotype with a beneficial effect on fitness.

- Many mutations, called neutral mutations, will have no effect on fitness.

Mutations may also have a whole range of effect sizes on the fitness of the organism that expresses them in their phenotype, from a small effect to a great effect. Sexual reproduction and crossing over in meiosis also lead to genetic diversity: when two parents reproduce, unique combinations of alleles assemble to produce unique genotypes and, thus, phenotypes in each of the offspring.

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an **adaptation**. An adaptation is a “match” of the organism to the environment. Adaptation to an environment comes about when a change in the range of genetic variation occurs over time that increases or maintains the match of the population with its environment. The variations in finch beaks shifted from generation to generation providing adaptation to food availability.

Whether or not a trait is favorable depends on the environment at the time. The same traits do not always have the same relative benefit or disadvantage because environmental conditions can change. For example, finches with large bills were benefited in one climate, while small bills were a disadvantage; in a different climate, the relationship reversed.

Patterns of Evolution

The evolution of species has resulted in enormous variation in form and function. When two species evolve in different directions from a common point, it is called **divergent evolution**. Such divergent evolution can be seen in the forms of the reproductive organs of flowering plants, which share the same basic anatomies; however, they can look very different as a result of selection in different physical environments, and adaptation to different kinds of pollinators ([\[link\]](#)).



(a)



(b)

Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star and (b) purple coneflower vary in appearance, yet both share a similar basic morphology. (credit a, b: modification of work by Cory Zanker)

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. The wings of bats and insects, however, evolved from very different original structures. When similar structures arise through evolution independently in different species it is called **convergent evolution**. The wings of bats and insects are called **analogous structures**; they are similar in function and appearance, but do not share an origin in a common ancestor. Instead they evolved independently in the two lineages. The wings of a hummingbird and an ostrich are **homologous structures**, meaning they share similarities (despite their differences resulting from evolutionary divergence). The wings of hummingbirds and ostriches did not evolve independently in the hummingbird lineage and the ostrich lineage—they descended from a common ancestor with wings.

The Modern Synthesis

The mechanisms of inheritance, genetics, were not understood at the time Darwin and Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to comprehending many

aspects of evolution. In fact, blending inheritance was the predominant (and incorrect) genetic theory of the time, which made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after publication of *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades genetics and evolution were integrated in what became known as the **modern synthesis**—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary pressures, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this gradual change of a population over time, called **microevolution**, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called **macroevolution**.

Population Genetics

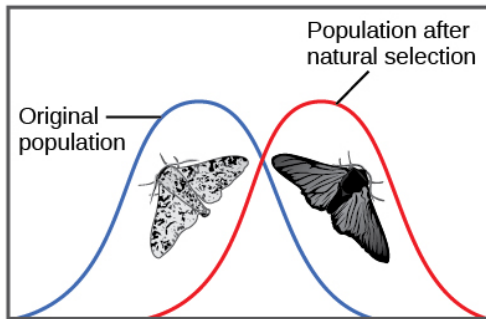
Recall that a gene for a particular character may have several variants, or alleles, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type protein on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that make up the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists began to study what happens to all the alleles in a population in a field of study known as **population genetics**.

Until now, we have defined evolution as a change in the characteristics of a population of organisms, but behind that phenotypic change is genetic change. In population genetic terms, evolution is defined as a change in the frequency of an allele in a population. Using the ABO system as an

example, the frequency of one of the alleles, I^A , is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan found a frequency of I^A to be 26.1 percent. [\[footnote\]](#) The I^B , I^O alleles made up 13.4 percent and 60.5 percent of the alleles respectively, and all of the frequencies add up to 100 percent. A change in this frequency over time would constitute evolution in the population.

Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, “Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population,” *Journal of Medical Sciences* 7 (2007): 51-58, doi:10.3923/jms.2007.51.58

There are several ways the allele frequencies of a population can change. One of those ways is natural selection. If a given allele confers a phenotype that allows an individual to have more offspring that survive and reproduce, that allele, by virtue of being inherited by those offspring, will be in greater frequency in the next generation. Since allele frequencies always add up to 100 percent, an increase in the frequency of one allele always means a corresponding decrease in one or more of the other alleles. Highly beneficial alleles may, over a very few generations, become “fixed” in this way, meaning that every individual of the population will carry the allele. Similarly, detrimental alleles may be swiftly eliminated from the **gene pool**, the sum of all the alleles in a population. Part of the study of population genetics is tracking how selective forces change the allele frequencies in a population over time, which can give scientists clues regarding the selective forces that may be operating on a given population. The studies of changes in wing coloration in the peppered moth from mottled white to dark in response to soot-covered tree trunks and then back to mottled white when factories stopped producing so much soot is a classic example of studying evolution in natural populations ([\[link\]](#)).



Light-colored peppered moths are better camouflaged against a pristine environment; likewise, dark-colored peppered moths are better camouflaged against a sooty environment. Thus, as the Industrial Revolution progressed in nineteenth-century England, the color of the moth population shifted from light to dark.

As the Industrial Revolution caused trees to darken from soot, darker colored peppered moths were better camouflaged than the lighter colored ones, which caused there to be more of the darker colored moths in the population.

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg independently provided an explanation for a somewhat counterintuitive concept. Hardy's original explanation was in response to a misunderstanding as to why a "dominant" allele, one that masks a recessive allele, should not increase in frequency in a population until it eliminated all the other alleles. The question resulted from a common confusion about what "dominant" means, but it forced Hardy, who was not even a biologist, to point out that if there are no factors that affect an allele frequency those frequencies will remain constant from one generation to the next. This principle is now known as the Hardy-Weinberg equilibrium. The theory states that a population's allele and genotype frequencies are inherently stable—unless some kind of evolutionary force is acting on the population, the population would carry the same alleles in the same proportions generation after generation. Individuals would, as a whole, look essentially the same and this would be unrelated to whether the alleles were dominant or recessive. The four most important evolutionary forces, which will disrupt the equilibrium, are natural selection, mutation, **genetic drift**, and **migration** into or out of a population. A fifth factor, nonrandom mating, will also disrupt the Hardy-Weinberg equilibrium but only by shifting genotype frequencies, not allele frequencies. In nonrandom mating, individuals are more likely to mate with

like individuals (or unlike individuals) rather than at random. Since nonrandom mating does not change allele frequencies, it does not cause evolution directly. Natural selection has been described. Mutation creates one allele out of another one and changes an allele's frequency by a small, but continuous amount each generation. Each allele is generated by a low, constant mutation rate that will slowly increase the allele's frequency in a population if no other forces act on the allele. If natural selection acts against the allele, it will be removed from the population at a low rate leading to a frequency that results from a balance between selection and mutation. This is one reason that genetic diseases remain in the human population at very low frequencies. If the allele is favored by selection, it will increase in frequency. Genetic drift causes random changes in allele frequencies when populations are small. Genetic drift can often be important in evolution, as discussed in the next section. Finally, if two populations of a species have different allele frequencies, migration of individuals between them will cause frequency changes in both populations. As it happens, there is no population in which one or more of these processes are not operating, so populations are always evolving, and the Hardy-Weinberg equilibrium will never be exactly observed. However, the Hardy-Weinberg principle gives scientists a baseline expectation for allele frequencies in a non-evolving population to which they can compare evolving populations and thereby infer what evolutionary forces might be at play. The population is evolving if the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg principle.

Darwin identified a special case of natural selection that he called sexual selection. Sexual selection affects an individual's ability to mate and thus produce offspring, and it leads to the evolution of dramatic traits that often appear maladaptive in terms of survival but persist because they give their owners greater reproductive success. Sexual selection occurs in two ways: through male–male competition for mates and through female selection of mates. Male–male competition takes the form of conflicts between males, which are often ritualized, but may also pose significant threats to a male's survival. Sometimes the competition is for territory, with females more likely to mate with males with higher quality territories. Female choice occurs when females choose a male based on a particular trait, such as feather colors, the performance of a mating dance, or the building of an

elaborate structure. In some cases male–male competition and female choice combine in the mating process. In each of these cases, the traits selected for, such as fighting ability or feather color and length, become enhanced in the males. In general, it is thought that sexual selection can proceed to a point at which natural selection against a character's further enhancement prevents its further evolution because it negatively impacts the male's ability to survive. For example, colorful feathers or an elaborate display make the male more obvious to predators.

Section Summary

Evolution by natural selection arises from three conditions: individuals within a species vary, some of those variations are heritable, and organisms have more offspring than resources can support. The consequence is that individuals with relatively advantageous variations will be more likely to survive and have higher reproductive rates than those individuals with different traits. The advantageous traits will be passed on to offspring in greater proportion. Thus, the trait will have higher representation in the next and subsequent generations leading to genetic change in the population.

The modern synthesis of evolutionary theory grew out of the reconciliation of Darwin's, Wallace's, and Mendel's thoughts on evolution and heredity. Population genetics is a theoretical framework for describing evolutionary change in populations through the change in allele frequencies. Population genetics defines evolution as a change in allele frequency over generations. In the absence of evolutionary forces allele frequencies will not change in a population; this is known as Hardy-Weinberg equilibrium principle. However, in all populations, mutation, natural selection, genetic drift, and migration act to change allele frequencies.

Multiple Choice

Exercise:

Problem:

Which scientific concept did Charles Darwin and Alfred Wallace independently discover?

- a. mutation
- b. natural selection
- c. overbreeding
- d. sexual reproduction

Solution:

B

Exercise:**Problem:**

Which of the following situations will lead to natural selection?

- a. The seeds of two plants land near each other and one grows larger than the other.
- b. Two types of fish eat the same kind of food, and one is better able to gather food than the other.
- c. Male lions compete for the right to mate with females, with only one possible winner.
- d. all of the above

Solution:

D

Exercise:

Problem: What is the difference between micro- and macroevolution?

- a. Microevolution describes the evolution of small organisms, such as insects, while macroevolution describes the evolution of large organisms, like people and elephants.
- b. Microevolution describes the evolution of microscopic entities, such as molecules and proteins, while macroevolution describes the evolution of whole organisms.
- c. Microevolution describes the evolution of populations, while macroevolution describes the emergence of new species over long periods of time.
- d. Microevolution describes the evolution of organisms over their lifetimes, while macroevolution describes the evolution of organisms over multiple generations.

Solution:

C

Exercise:

Problem: Population genetics is the study of _____.

- a. how allele frequencies in a population change over time
- b. populations of cells in an individual
- c. the rate of population growth
- d. how genes affect embryological development

Solution:

A

Free Response

Exercise:

Problem:

If a person scatters a handful of plant seeds from one species in an area, how would natural selection work in this situation?

Solution:

The plants that can best use the resources of the area, including competing with other individuals for those resources, will produce more seeds themselves and those traits that allowed them to better use the resources will increase in the population of the next generation.

Exercise:

Problem: Explain the Hardy-Weinberg principle of equilibrium.

Solution:

The Hardy-Weinberg principle of equilibrium states that a population's allele frequencies are inherently stable. Unless an evolutionary force is acting upon the population, the population would carry the same genes at the same frequencies generation after generation, and individuals would, as a whole, look essentially the same.

Glossary**adaptation**

a heritable trait or behavior in an organism that aids in its survival in its present environment

analogous structure

a structure that is similar because of evolution in response to similar selection pressures resulting in convergent evolution, not similar because of descent from a common ancestor

convergent evolution

an evolution that results in similar forms on different species

divergent evolution

an evolution that results in different forms in two species with a common ancestor

gene pool

all of the alleles carried by all of the individuals in the population

genetic drift

the effect of chance on a population's gene pool

homologous structure

a structure that is similar because of descent from a common ancestor

inheritance of acquired characteristics

a phrase that describes the mechanism of evolution proposed by Lamarck in which traits acquired by individuals through use or disuse could be passed on to their offspring thus leading to evolutionary change in the population

macroevolution

a broader scale of evolutionary changes seen over paleontological time

microevolution

the changes in a population's genetic structure (i.e., allele frequency)

migration

the movement of individuals of a population to a new location; in population genetics it refers to the movement of individuals and their alleles from one population to another, potentially changing allele frequencies in both the old and the new population

modern synthesis

the overarching evolutionary paradigm that took shape by the 1940s and is generally accepted today

natural selection

the greater relative survival and reproduction of individuals in a population that have favorable heritable traits, leading to evolutionary

change

population genetics

the study of how selective forces change the allele frequencies in a population over time

variation

the variety of alleles in a population

Mechanisms of Evolution

By the end of this section, you will be able to:

- Describe the four basic causes of evolution: natural selection, mutation, genetic drift, and gene flow
- Explain how each evolutionary force can influence the allele frequencies of a population

The Hardy-Weinberg equilibrium principle says that allele frequencies in a population will remain constant in the absence of the four factors that could change them. Those factors are natural selection, mutation, genetic drift, and migration (gene flow). In fact, we know they are probably always affecting populations.

Natural Selection

Natural selection has already been discussed. Alleles are expressed in a phenotype. Depending on the environmental conditions, the phenotype confers an advantage or disadvantage to the individual with the phenotype relative to the other phenotypes in the population. If it is an advantage, then that individual will likely have more offspring than individuals with the other phenotypes, and this will mean that the allele behind the phenotype will have greater representation in the next generation. If conditions remain the same, those offspring, which are carrying the same allele, will also benefit. Over time, the allele will increase in frequency in the population.

Mutation

Mutation is a source of new alleles in a population. Mutation is a change in the DNA sequence of the gene. A mutation can change one allele into another, but the net effect is a change in frequency. The change in frequency resulting from mutation is small, so its effect on evolution is small unless it interacts with one of the other factors, such as selection. A mutation may produce an allele that is selected against, selected for, or selectively neutral. Harmful mutations are removed from the population by selection and will generally only be found in very low frequencies equal to the mutation rate. Beneficial mutations will spread through the population through selection,

although that initial spread is slow. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. It should be noted that mutation is the ultimate source of genetic variation in all populations—new alleles, and, therefore, new genetic variations arise through mutation.

Genetic Drift

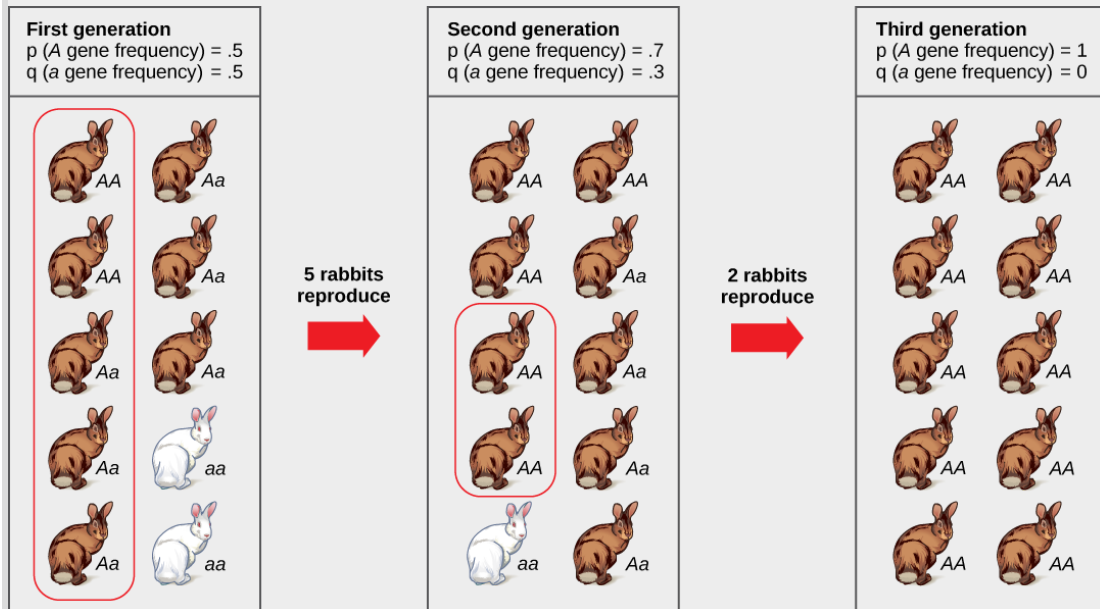
Another way a population's allele frequencies can change is genetic drift ([link](#)), which is simply the effect of chance. Genetic drift is most important in small populations. Drift would be completely absent in a population with infinite individuals, but, of course, no population is this large. Genetic drift occurs because the alleles in an offspring generation are a random sample of the alleles in the parent generation. Alleles may or may not make it into the next generation due to chance events including mortality of an individual, events affecting finding a mate, and even the events affecting which gametes end up in fertilizations. If one individual in a population of ten individuals happens to die before it leaves any offspring to the next generation, all of its genes—a tenth of the population's gene pool—will be suddenly lost. In a population of 100, that 1 individual represents only 1 percent of the overall gene pool; therefore, it has much less impact on the population's genetic structure and is unlikely to remove all copies of even a relatively rare allele.

Imagine a population of ten individuals, half with allele *A* and half with allele *a* (the individuals are haploid). In a stable population, the next generation will also have ten individuals. Choose that generation randomly by flipping a coin ten times and let heads be *A* and tails be *a*. It is unlikely that the next generation will have exactly half of each allele. There might be six of one and four of the other, or some different set of frequencies. Thus, the allele frequencies have changed and evolution has occurred. A coin will no longer work to choose the next generation (because the odds are no longer one half for each allele). The frequency in each generation will drift up and down on what is known as a random walk until at one point either all *A* or all *a* are chosen and that allele is fixed from that point on. This could take a very long time for a large population. This simplification is not very biological, but it can be shown that real populations behave this way.

The effect of drift on frequencies is greater the smaller a population is. Its effect is also greater on an allele with a frequency far from one half. Drift will influence every allele, even those that are being naturally selected.

Note:

Art Connection

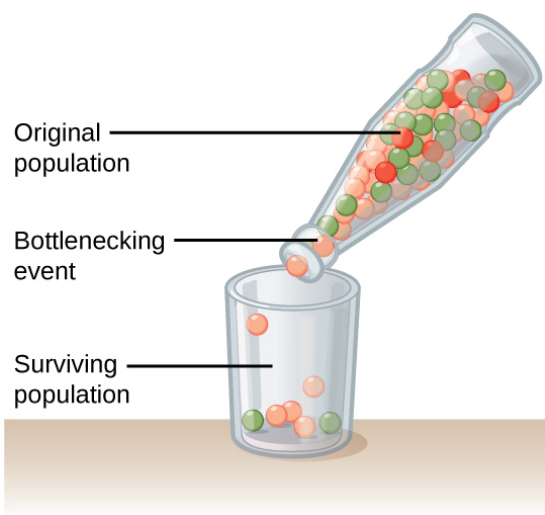


Genetic drift in a population can lead to the elimination of an allele from a population by chance. In each generation, a random set of individuals reproduces to produce the next generation. The frequency of alleles in the next generation is equal to the frequency of alleles among the individuals reproducing.

Do you think genetic drift would happen more quickly on an island or on the mainland?

Genetic drift can also be magnified by natural or human-caused events, such as a disaster that randomly kills a large portion of the population,

which is known as the **bottleneck effect** that results in a large portion of the genome suddenly being wiped out ([link](#)). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population. The disaster must be one that kills for reasons unrelated to the organism's traits, such as a hurricane or lava flow. A mass killing caused by unusually cold temperatures at night, is likely to affect individuals differently depending on the alleles they possess that confer cold hardiness.



A chance event or catastrophe can reduce the genetic variability within a population.

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location, or if a population gets divided by a physical barrier of some kind. In this situation, those individuals are unlikely to be representative of the entire population which results in the **founder effect**. The founder effect occurs when the genetic structure matches that of the new population's founding fathers and mothers. The founder effect is

believed to have been a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This is likely due to a higher-than-normal proportion of the founding colonists, which were a small sample of the original population, carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause bone marrow and congenital abnormalities, and even cancer. [\[footnote\]](#)

A. J. Tipping et al., "Molecular and Genealogical Evidence for a Founder Effect in Fanconi Anemia Families of the Afrikaner Population of South Africa," *PNAS* 98, no. 10 (2001): 5734-5739, doi: 10.1073/pnas.091402398.

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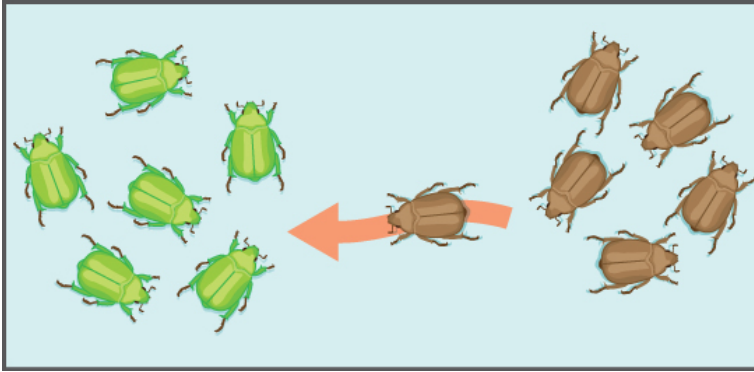
Concept in Action



Visit this [site](#) to learn more about genetic drift and to run simulations of allele changes caused by drift.

Gene Flow

Another important evolutionary force is **gene flow**, or the flow of alleles in and out of a population resulting from the migration of individuals or gametes ([\[link\]](#)). While some populations are fairly stable, others experience more flux. Many plants, for example, send their seeds far and wide, by wind or in the guts of animals; these seeds may introduce alleles common in the source population to a new population in which they are rare.



Gene flow can occur when an individual travels from one geographic location to another and joins a different population of the species. In the example shown here, the brown allele is introduced into the green population.

Section Summary

There are four factors that can change the allele frequencies of a population. Natural selection works by selecting for alleles that confer beneficial traits or behaviors, while selecting against those for deleterious qualities. Mutations introduce new alleles into a population. Genetic drift stems from the chance occurrence that some individuals have more offspring than others and results in changes in allele frequencies that are random in direction. When individuals leave or join the population, allele frequencies can change as a result of gene flow.

Art Connections

Exercise:

Problem:

[\[link\]](#) Do you think genetic drift would happen more quickly on an island or on the mainland?

Solution:

[\[link\]](#) Genetic drift is likely to occur more rapidly on an island, where smaller populations are expected to occur.

Multiple Choice**Exercise:****Problem:**

Galápagos medium ground finches are found on Santa Cruz and San Cristóbal islands, which are separated by about 100 km of ocean. Occasionally, individuals from either island fly to the other island to stay. This can alter the allele frequencies of the population through which of the following mechanisms?

- a. natural selection
- b. genetic drift
- c. gene flow
- d. mutation

Solution:

C

Exercise:**Problem:**

In which of the following pairs do both evolutionary processes introduce new genetic variation into a population?

- a. natural selection and genetic drift
- b. mutation and gene flow
- c. natural selection and gene flow
- d. gene flow and genetic drift

Solution:

B

Free Response**Exercise:****Problem:**

Describe natural selection and give an example of natural selection at work in a population.

Solution:

The theory of natural selection stems from the observation that some individuals in a population survive longer and have more offspring than others, thus passing on more of their genes to the next generation. For example, a big, powerful male gorilla is much more likely than a smaller, weaker gorilla to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will, therefore, father more offspring, who share half of his genes, and are thus likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average.

Glossary

bottleneck effect

the magnification of genetic drift as a result of natural events or catastrophes

founder effect

a magnification of genetic drift in a small population that migrates away from a large parent population carrying with it an unrepresentative set of alleles

gene flow

the flow of alleles in and out of a population due to the migration of individuals or gametes

Evidence of Evolution

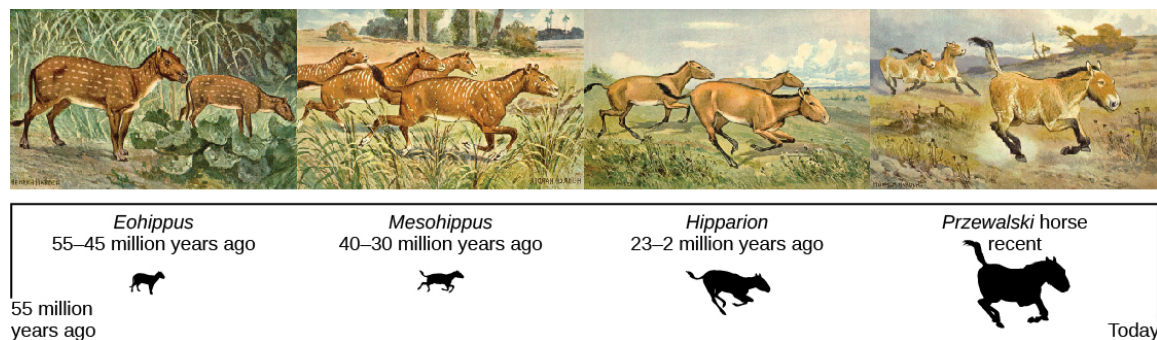
By the end of this section, you will be able to:

- Explain sources of evidence for evolution
- Define homologous and vestigial structures

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, identifying patterns in nature that were consistent with evolution and since Darwin our understanding has become clearer and broader.

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today; fossils show a progression of evolution. Scientists determine the age of fossils and categorize them all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past, and shows the evolution of form over millions of years ([\[link\]](#)). For example, highly detailed fossil records have been recovered for sequences of species in the evolution of whales and modern horses. The fossil record of horses in North America is especially rich and many contain transition fossils: those showing intermediate anatomy between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago that gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*. The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested one to a prairie. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit, with adaptations for escaping predators, for example in species of *Mesohippus* found from 40 to 30 million years ago. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species.

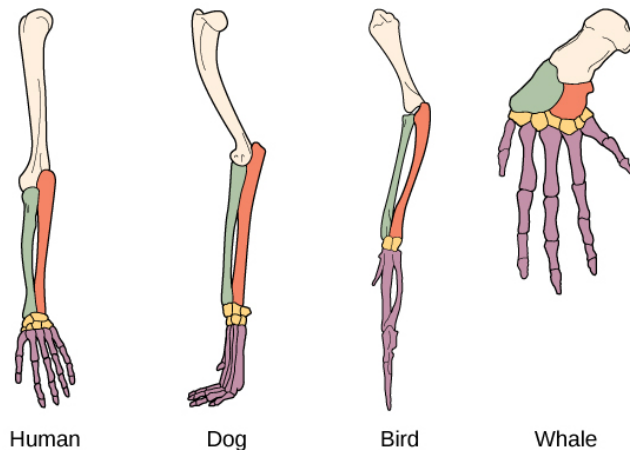


This illustration shows an artist's renderings of these species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running. Przewalski's horse is one of a few living species of horse.

Anatomy and Embryology

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction ([link](#)). That similarity results from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout, evidence of descent from a common ancestor. Scientists call these synonymous parts homologous structures. Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. These unused structures without function are called **vestigial structures**. Other examples of vestigial structures are wings

on flightless birds (which may have other functions), leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.



The similar construction of these appendages indicates that these organisms share a common ancestor.

Note:

Concept in Action



Click through the activities at this [interactive site](#) to guess which bone structures are homologous and which are analogous, and to see examples of all kinds of evolutionary adaptations that illustrate these concepts.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan (a bird), living in the arctic region have temporary white coverings during winter to blend with the snow and ice ([link](#)). The similarity occurs not because of common ancestry, indeed one covering is of fur and the other of feathers, but because of similar selection pressures—the benefits of not being seen by predators.



(a)



(b)

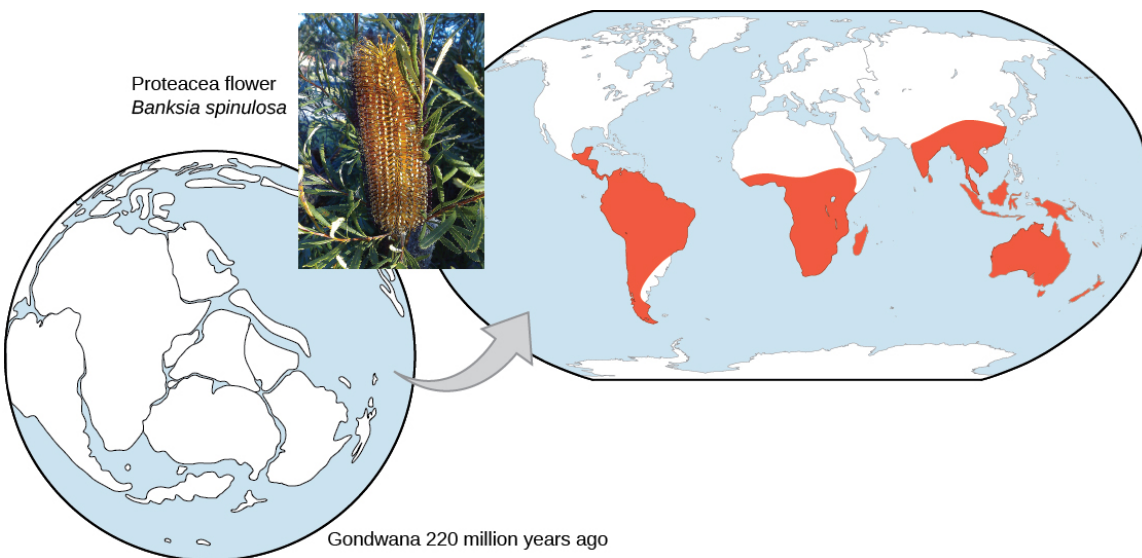
The white winter coat of (a) the arctic fox and (b) the ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)

Embryology, the study of the development of the anatomy of an organism to its adult form also provides evidence of relatedness between now widely divergent groups of organisms. Structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits at some point in their early development. These disappear in the adults of terrestrial groups, but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape

embryos, including humans, have a tail structure during their development that is lost by the time of birth. The reason embryos of unrelated species are often similar is that mutational changes that affect the organism during embryonic development can cause amplified differences in the adult, even while the embryonic similarities are preserved.

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, for example the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of Proteaceae in Australia, southern Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up ([\[link\]](#)).



The Proteaceae family of plants evolved before the supercontinent Gondwana broke up. Today, members of this plant family are

found throughout the southern hemisphere (shown in red). (credit “Proteacea flower”: modification of work by “dorofofoto”/Flickr)

The great diversification of the marsupials in Australia and the absence of other mammals reflects that island continent’s long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents migration of species to other regions. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all found nowhere else but on their island, yet display distant relationships to ancestral species on mainlands.

Molecular Biology

Like anatomical structures, the structures of the molecules of life reflect descent with modification. Evidence of a common ancestor for all of life is reflected in the universality of DNA as the genetic material and of the near universality of the genetic code and the machinery of DNA replication and expression. Fundamental divisions in life between the three domains are reflected in major structural differences in otherwise conservative structures such as the components of ribosomes and the structures of membranes. In general, the relatedness of groups of organisms is reflected in the similarity of their DNA sequences—exactly the pattern that would be expected from descent and diversification from a common ancestor.

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events. These duplications are a kind of mutation in which an entire gene is added as an extra copy (or many copies) in the genome. These duplications allow the free modification of one copy by mutation, selection, and drift, while the second copy continues to produce a functional protein. This allows the original function

for the protein to be kept, while evolutionary forces tweak the copy until it functions in a new way.

Section Summary

The evidence for evolution is found at all levels of organization in living things and in the extinct species we know about through fossils. Fossils provide evidence for the evolutionary change through now extinct forms that led to modern species. For example, there is a rich fossil record that shows the evolutionary transitions from horse ancestors to modern horses that document intermediate forms and a gradual adaptation o changing ecosystems. The anatomy of species and the embryological development of that anatomy reveal common structures in divergent lineages that have been modified over time by evolution. The geographical distribution of living species reflects the origins of species in particular geographic locations and the history of continental movements. The structures of molecules, like anatomical structures, reflect the relationships of living species and match patterns of similarity expected from descent with modification.

Multiple Choice

Exercise:

Problem:

The wing of a bird and the arm of a human are examples of _____.

- a. vestigial structures
- b. molecular structures
- c. homologous structures
- d. analogous structures

Solution:

C

Exercise:

Problem:

The fact that DNA sequences are more similar in more closely related organisms is evidence of what?

- a. optimal design in organisms
- b. adaptation
- c. mutation
- d. descent with modification

Solution:

D

Free Response**Exercise:****Problem:**

Why do scientists consider vestigial structures evidence for evolution?

Solution:

A vestigial structure is an example of a homologous structure that has apparently been reduced through evolution to a non-functional state because its function is no longer utilized by the species exhibiting it; therefore, any mutations which might reduce its structure are not selected against. The fact that the species has vestiges of the structure rather than no structure at all is evidence that it was present in an ancestor and evolved to non-functionality through accumulation of random mutations.

Glossary

vestigial structure

a physical structure present in an organism but that has no apparent function and appears to be from a functional structure in a distant ancestor

Speciation

By the end of this section, you will be able to:

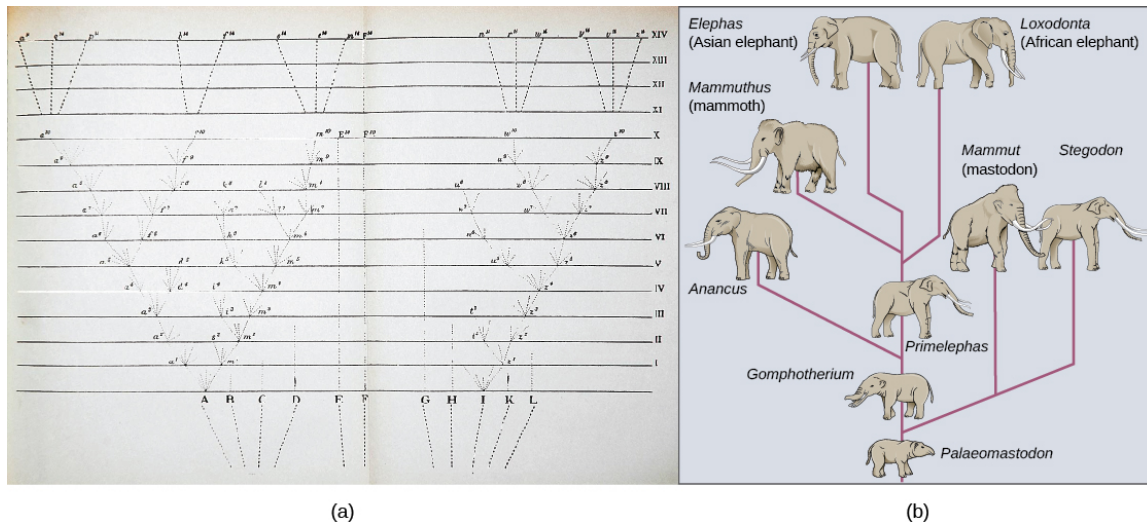
- Describe the definition of species and how species are identified as different
- Explain allopatric and sympatric speciation
- Describe adaptive radiation

The biological definition of species, which works for sexually reproducing organisms, is a group of actually or potentially interbreeding individuals. According to this definition, one species is distinguished from another by the possibility of matings between individuals from each species to produce fertile offspring. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. In fact, the presence of hybrids between similar species suggests that they may have descended from a single interbreeding species and that the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* ([link](#)). For speciation to occur, two new populations must be formed from one original population, and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation**, meaning speciation in “other homelands,” involves a geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation**, meaning speciation in the “same homeland,” involves speciation occurring within a parent species while remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely and

such multiple events can also be conceptualized as single splits occurring close in time.



The only illustration in Darwin's *On the Origin of Species* is (a) a diagram showing speciation events leading to biological diversity.

The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the *Palaeomastodon*, a species that lived in Egypt 35–50 million years ago.

Speciation through Geographic Separation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of a distribution will be similar to the frequency of the allele at the other end. When populations become geographically discontinuous that free-flow of alleles is prevented. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become more and more different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources,

predators, and competitors, for the two populations will differ causing natural selection to favor divergent adaptations in each group. Different histories of genetic drift, enhanced because the populations are smaller than the parent population, will also lead to divergence.

Given enough time, the genetic and phenotypic divergence between populations will likely affect characters that influence reproduction enough that were individuals of the two populations brought together, mating would be less likely, or if a mating occurred, offspring would be non-viable or infertile. Many types of diverging characters may affect the reproductive isolation (inability to interbreed) of the two populations. These mechanisms of reproductive isolation can be divided into prezygotic mechanisms (those that operate before fertilization) and postzygotic mechanisms (those that operate after fertilization). Prezygotic mechanisms include traits that allow the individuals to find each other, such as the timing of mating, sensitivity to pheromones, or choice of mating sites. If individuals are able to encounter each other, character divergence may prevent courtship rituals from leading to a mating either because female preferences have changed or male behaviors have changed. Physiological changes may interfere with successful fertilization if mating is able to occur. Postzygotic mechanisms include genetic incompatibilities that prevent proper development of the offspring, or if the offspring live, they may be unable to produce viable gametes themselves as in the example of the mule, the infertile offspring of a female horse and a male donkey.

If the two isolated populations are brought back together and the hybrid offspring that formed from matings between individuals of the two populations have lower survivorship or reduced fertility, then selection will favor individuals that are able to discriminate between potential mates of their own population and the other population. This selection will enhance the reproductive isolation.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: from a river forming a new branch, erosion forming a new valley, or a group of organisms traveling to a new location without the ability to return, such as seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations

depends entirely on the biology of the organism and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are that individuals from each population would fly back and forth, continuing gene flow. However, if two rodent populations became divided by the formation of a new lake, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories. If a few members of a species move to a new geographical area, this is called **dispersal**. If a natural situation arises to physically divide organisms, this is called **vicariance**.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate subspecies of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south ([\[link\]](#)). The cause of their initial separation is not clear, but it may have been caused by the glaciers of the ice age dividing an initial population into two. [\[footnote\]](#)

Courtney, S.P., et al, “Scientific Evaluation of the Status of the Northern Spotted Owl,” Sustainable Ecosystems Institute (2004), Portland, OR.

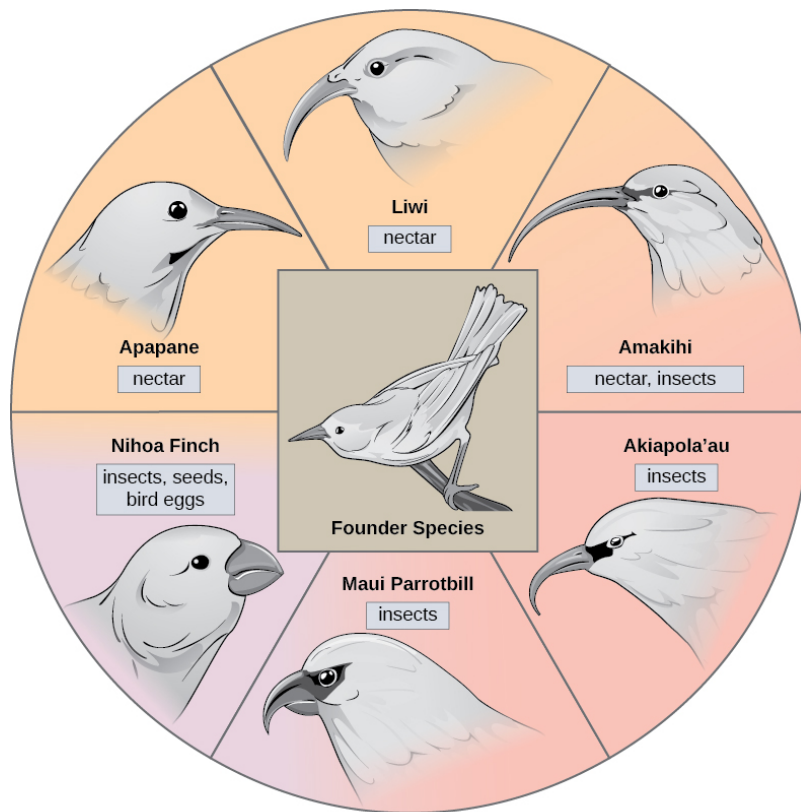


The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of incipient speciation.
(credit “northern spotted owl”: modification of work by John and Karen Hollingsworth, USFWS; credit “Mexican spotted owl”: modification of work by Bill Radke, USFWS)

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely for speciation to take place. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls; in the north, the climate is cooler

than in the south; the other types of organisms in each ecosystem differ, as do their behaviors and habits; also, the hunting habits and prey choices of the owls in the south vary from the northern ones. These variances can lead to evolved differences in the owls, and over time speciation will likely occur unless gene flow between the populations is restored.

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species, which is called **adaptive radiation**. From one point of origin, many adaptations evolve causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island, which leads to geographical isolation for many organisms ([\[link\]](#)). The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, called the founder species, numerous species have evolved, including the eight shown in [\[link\]](#).



The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in [\[link\]](#). Change in the genetic variation for beaks in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The fruit and seed-eating birds have thicker, stronger beaks which are suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach their nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another well-studied example of adaptive radiation in an archipelago.

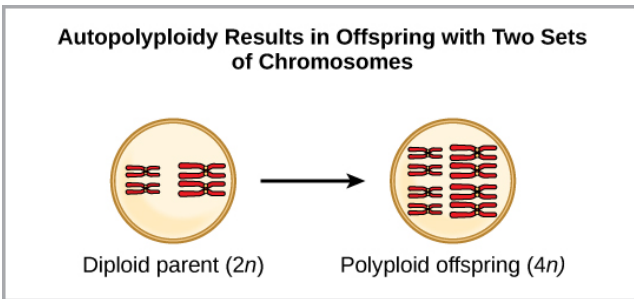
Note:**Concept in Action**

Click through this [interactive site](#) to see how island birds evolved; click to see images of each species in evolutionary increments from five million years ago to today.

Speciation without Geographic Separation

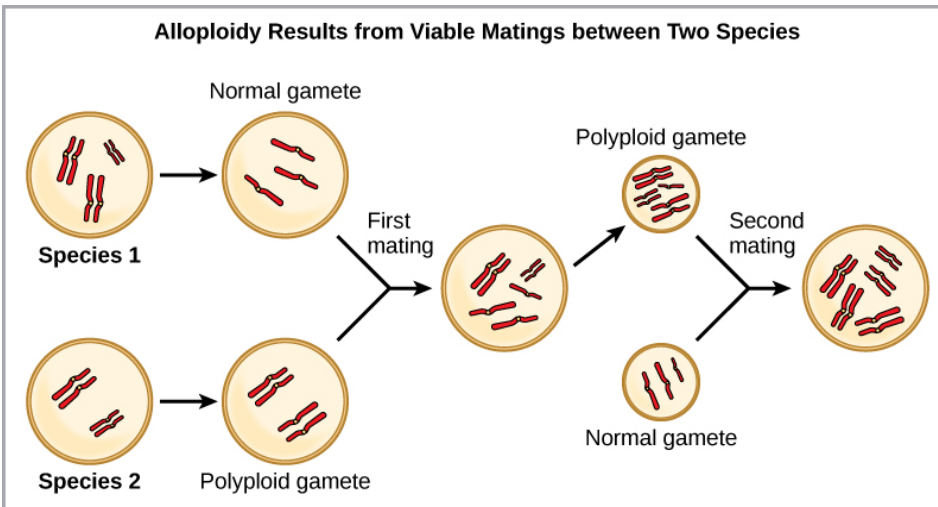
Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? A number of mechanisms for sympatric speciation have been proposed and studied.

One form of sympatric speciation can begin with a chromosomal error during meiosis or the formation of a hybrid individual with too many chromosomes. Polyploidy is a condition in which a cell, or organism, has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploid state. In some cases a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition called autopolyploidy ([link](#)). The prefix “auto” means self, so the term means multiple chromosomes from one’s own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.



Autopolyploidy results when
mitosis is not followed by
cytokinesis.

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes produced by this plant species. But they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ called a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species. The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an allopolyploid. The prefix “allo” means “other” (recall from allopatric); therefore, an allopolyploid occurs when gametes from two different species combine. [\[link\]](#) illustrates one possible way an allopolyploidy can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.



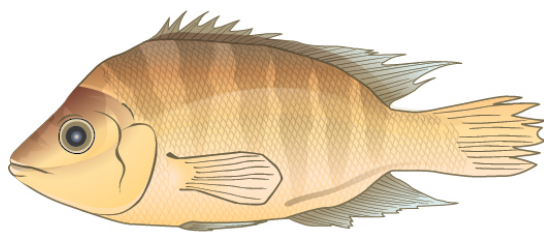
Allopolyploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploid gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, most chromosomal abnormalities in animals are lethal; it takes place most commonly in plants. Scientists have discovered more than 1/2 of all plant species studied relate back to a species evolved through polyploidy.

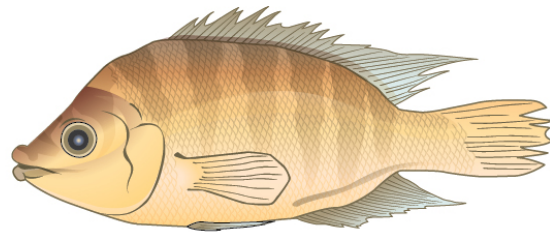
Sympatric speciation may also take place in ways other than polyploidy. For example, imagine a species of fish that lived in a lake. As the population grew, competition for food also grew. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore they would breed together as well. Offspring of these fish would likely behave as their parents and feed and live in the same area, keeping them separate from the original population. If this group of fish continued to remain separate from the first

population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. [\[link\]](#) shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location; however, they have come to have different morphologies that allow them to eat various food sources.



Thin-lipped cichlid



Thick-lipped cichlid

Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish.

Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

Finally, a well-documented example of ongoing sympatric speciation occurred in the apple maggot fly, *Rhagoletis pomonella*, which arose as an isolated population sometime after the introduction of the apple into North America. The native population of flies fed on hawthorn species and is host-specific: it only infests hawthorn trees. Importantly, it also uses the trees as a location to meet for mating. It is hypothesized that either through

mutation or a behavioral mistake, flies jumped hosts and met and mated in apple trees, subsequently laying their eggs in apple fruit. The offspring matured and kept their preference for the apple trees effectively dividing the original population into two new populations separated by host species, not by geography. The host jump took place in the nineteenth century, but there are now measureable differences between the two populations of fly. It seems likely that host specificity of parasites in general is a common cause of sympatric speciation.

Section Summary

Speciation occurs along two main pathways: geographic separation (allopatric speciation) and through mechanisms that occur within a shared habitat (sympatric speciation). Both pathways force reproductive isolation between populations. Sympatric speciation can occur through errors in meiosis that form gametes with extra chromosomes, called polyploidy. Autopolyploidy occurs within a single species, whereas allopolyploidy occurs because of a mating between closely related species. Once the populations are isolated, evolutionary divergence can take place leading to the evolution of reproductive isolating traits that prevent interbreeding should the two populations come together again. The reduced viability of hybrid offspring after a period of isolation is expected to select for stronger inherent isolating mechanisms.

Multiple Choice

Exercise:

Problem:

Which situation would most likely lead to allopatric speciation?

- a. A flood causes the formation of a new lake.
 - b. A storm causes several large trees to fall down.
 - c. A mutation causes a new trait to develop.
 - d. An injury causes an organism to seek out a new food source.
-

Solution:

A

Exercise:

Problem:

What is the main difference between dispersal and vicariance?

- a. One leads to allopatric speciation, whereas the other leads to sympatric speciation.
 - b. One involves the movement of the organism, whereas the other involves a change in the environment.
 - c. One depends on a genetic mutation occurring, whereas the other does not.
 - d. One involves closely related organisms, whereas the other involves only individuals of the same species.
-

Solution:

B

Exercise:

Problem:

Which variable increases the likelihood of allopatric speciation taking place more quickly?

- a. lower rate of mutation
 - b. longer distance between divided groups
 - c. increased instances of hybrid formation
 - d. equivalent numbers of individuals in each population
-

Solution:

B

Free Response

Exercise:

Problem:

Why do island chains provide ideal conditions for adaptive radiation to occur?

Solution:

Organisms of one species can arrive to an island together and then disperse throughout the chain, each settling into different niches, exploiting different food resources and, evolving independently with little gene flow between different islands.

Exercise:

Problem:

Two species of fish had recently undergone sympatric speciation. The males of each species had a different coloring through which females could identify and choose a partner from her own species. After some time, pollution made the lake so cloudy it was hard for females to distinguish colors. What might take place in this situation?

Solution:

It is likely the two species would start to reproduce with each other if hybridization is still possible. Depending on the viability of their offspring, they may fuse back into one species.

Glossary

adaptive radiation

a speciation when one species radiates out to form several other species

allopatric speciation

a speciation that occurs via a geographic separation

dispersal

an allopatric speciation that occurs when a few members of a species move to a new geographical area

speciation

a formation of a new species

sympatric speciation

a speciation that occurs in the same geographic space

vicariance

an allopatric speciation that occurs when something in the environment separates organisms of the same species into separate groups

Common Misconceptions about Evolution

By the end of this section, you will be able to:

- Identify common misconceptions about evolution
- Identify common criticisms of evolution

Although the theory of evolution initially generated some controversy, by 20 years after the publication of *On the Origin of Species* it was almost universally accepted by biologists, particularly younger biologists. Nevertheless, the theory of evolution is a difficult concept and misconceptions about how it works abound. In addition, there are those that reject it as an explanation for the diversity of life.

Note:

Concept in Action



This [website](#) addresses some of the main misconceptions associated with the theory of evolution.

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word “theory” with the way scientists use the word. In science, a “theory” is understood to be a concept that has been extensively tested and supported over time. We have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes what scientists understand to be facts about the world. In the same way, the theory of evolution describes facts about the living world. As such,

a theory in science has survived significant efforts to discredit it by scientists, who are naturally skeptical. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly evolving state of scientific knowledge. In contrast, a “theory” in common vernacular means a guess or suggested explanation for something. This meaning is more akin to the concept of a “hypothesis” used by scientists, which is a tentative explanation for something that is proposed to either be supported or disproved. When critics of evolution say evolution is “just a theory,” they are implying that there is little evidence supporting it and that it is still in the process of being rigorously tested. This is a mischaracterization. If this were the case, geneticist Theodosius Dobzhansky would not have said that “nothing in biology makes sense, except in the light of evolution.”^{[[footnote](#)]} Theodosius Dobzhansky. “Biology, Molecular and Organismic.” *American Zoologist* 4, no. 4 (1964): 449.

Individuals Evolve

An individual is born with the genes it has—these do not change as the individual ages. Therefore, an individual cannot evolve or adapt through natural selection. Evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, but this is called development; it involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual’s environment. When thinking about the evolution of a characteristic, it is probably best to think about the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size change in medium ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time, and then measures the average bill size in the population several years later after there has been a strong selective pressure, this average value may be different as a result of evolution. Although some individuals may survive from the first time to the second, those individuals will still have the same bill size. However, there

may be enough new individuals with different bill sizes to change the average bill size.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics complain that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies—the origin of species. It does not shed light on the beginnings of life including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, over a very long time, and presumably just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things. The early stages of life included the formation of organic molecules such as carbohydrates, amino acids, or nucleotides. If these were formed from inorganic precursors today, they would simply be broken down by living things. The early stages of life also probably included more complex aggregations of molecules into enclosed structures with an internal environment, a boundary layer of some form, and the external environment. Such structures, if they were formed now, would be quickly consumed or broken down by living organisms.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA or RNA, either within a cell or within a pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Organisms Evolve on Purpose

Statements such as “organisms evolve in response to a change in an environment,” are quite common. There are two easy misunderstandings possible with such a statement. First of all, the statement must not be understood to mean that individual organisms evolve, as was discussed above. The statement is shorthand for “a population evolves in response to a changing environment.” However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and, therefore, producing proportionately more offspring than other phenotypes. This results in change in the population if the characters are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select for a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects for individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic application.

In a larger sense, evolution is also not goal directed. Species do not become “better” over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species. This kind of language is common in popular literature. Certain organisms, ourselves included, are described as the “pinnacle” of evolution, or “perfected” by evolution. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at

some point in the future. This holds equally well for a species of insect as it does the human species.

Evolution Is Controversial among Scientists

The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every working biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily rapid, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory and the arguments of religious leaders. It was the arguments of the biologists that were resolved after a short time, while the arguments of religious leaders have persisted to this day.

The theory of evolution replaced the predominant theory at the time that species had all been specially created within relatively recent history. Despite the prevalence of this theory, it was becoming increasingly clear to naturalists during the nineteenth century that it could no longer explain many observations of geology and the living world. The persuasiveness of the theory of evolution to these naturalists lay in its ability to explain these phenomena, and it continues to hold extraordinary explanatory power to this day. Its continued rejection by some religious leaders results from its replacement of special creation, a tenet of their religious belief. These leaders cannot accept the replacement of special creation by a mechanistic process that excludes the actions of a deity as an explanation for the diversity of life including the origins of the human species. It should be noted, however, that most of the major denominations in the United States have statements supporting the acceptance of evidence for evolution as compatible with their theologies.

The nature of the arguments against evolution by religious leaders has evolved over time. One current argument is that the theory is still controversial among biologists. This claim is simply not true. The number of working scientists who reject the theory of evolution, or question its validity and say so, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve. [\[footnote\]](#) The

support for the theory is reflected in signed statements from many scientific societies such as the American Association for the Advancement of Science, which includes working scientists as members. Many of the scientists that reject or question the theory of evolution are non-biologists, such as engineers, physicians, and chemists. There are no experimental results or research programs that contradict the theory. There are no papers published in peer-reviewed scientific journals that appear to refute the theory. The latter observation might be considered a consequence of suppression of dissent, but it must be remembered that scientists are skeptics and that there is a long history of published reports that challenged scientific orthodoxy in unpopular ways. Examples include the endosymbiotic theory of eukaryotic origins, the theory of group selection, the microbial cause of stomach ulcers, the asteroid-impact theory of the Cretaceous extinction, and the theory of plate tectonics. Research with evidence and ideas with scientific merit are considered by the scientific community. Research that does not meet these standards is rejected. Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.

Other Theories Should Be Taught

A common argument from some religious leaders is that alternative theories to evolution should be taught in public schools. Critics of evolution use this strategy to create uncertainty about the validity of the theory without offering actual evidence. In fact, there are no viable alternative scientific theories to evolution. The last such theory, proposed by Lamarck in the nineteenth century, was replaced by the theory of natural selection. A single exception was a research program in the Soviet Union based on Lamarck's theory during the early twentieth century that set that country's agricultural research back decades. Special creation is not a viable alternative scientific theory because it is not a scientific theory, since it relies on an untestable explanation. Intelligent design, despite the claims of its proponents, is also not a scientific explanation. This is because intelligent design posits the existence of an unknown designer of living organisms and their systems. Whether the designer is unknown or supernatural, it is a cause that cannot be measured; therefore, it is not a scientific explanation. There are two reasons not to teach nonscientific theories. First, these explanations for the

diversity of life lack scientific usefulness because they do not, and cannot, give rise to research programs that promote our understanding of the natural world. Experiments cannot test non-material explanations for natural phenomena. For this reason, teaching these explanations as science in public schools is not in the public interest. Second, in the United States, it is illegal to teach them as science because the U.S. Supreme Court and lower courts have ruled that the teaching of religious belief, such as special creation or intelligent design, violates the establishment clause of the First Amendment of the U.S. Constitution, which prohibits government sponsorship of a particular religion.

The theory of evolution and science in general is, by definition, silent on the existence or non-existence of the spiritual world. Science is only able to study and know the material world. Individual biologists have sometimes been vocal atheists, but it is equally true that there are many deeply religious biologists. Nothing in biology precludes the existence of a god, indeed biology as a science has nothing to say about it. The individual biologist is free to reconcile her or his personal and scientific knowledge as they see fit. The Voices for Evolution project (<http://ncse.com/voices>), developed through the National Center for Science Education, works to gather the diversity of perspectives on evolution to advocate it being taught in public schools.

Section Summary

The theory of evolution is a difficult concept and misconceptions abound. The factual nature of evolution is often challenged by wrongly associating the scientific meaning of a theory with the vernacular meaning. Evolution is sometimes mistakenly interpreted to mean that individuals evolve, when in fact only populations can evolve as their gene frequencies change over time. Evolution is often assumed to explain the origin of life, which it does not speak to. It is often spoken in goal-directed terms by which organisms change through intention, and selection operates on mutations present in a population that have not arisen in response to a particular environmental stress. Evolution is often characterized as being controversial among scientists; however, it is accepted by the vast majority of working scientists. Critics of evolution often argue that alternative theories to evolution should

be taught in public schools; however, there are no viable alternative scientific theories to evolution. The alternative religious beliefs should not be taught as science because it cannot be proven, and in the United States it is unconstitutional. Science is silent on the question of the existence of a god while scientists are able to reconcile religious belief and scientific knowledge.

Multiple Choice

Exercise:

Problem:

The word “theory” in theory of evolution is best replaced by _____.

- a. fact
- b. hypothesis
- c. idea
- d. alternate explanation

Solution:

A

Exercise:

Problem:

Why are alternative scientific theories to evolution not taught in public school?

- a. more theories would confuse students
 - b. there are no viable scientific alternatives
 - c. it is against the law
 - d. alternative scientific theories are suppressed by the science establishment
-

Solution:

B

Free Response**Exercise:****Problem:**

How does the scientific meaning of “theory” differ from the common, everyday meaning of the word?

Solution:

In science, a theory is a thoroughly tested and verified set of explanations for a body of observations of nature. It is the strongest form of knowledge in science. In contrast, a theory in common usage can mean a guess or speculation about something, meaning that the knowledge implied by the theory may be very weak.

Exercise:**Problem:**

Explain why the statement that a monkey is more evolved than a mouse is incorrect.

Solution:

The statement implies that there is a goal to evolution and that the monkey represents greater progress to that goal than the mouse. Both species are likely to be well adapted to their particular environment, which is the outcome of natural selection.

Introduction

class="introduction"

An arctic fox
is a complex
animal, well
adapted to
its
environment
. (credit:
Keith
Morehouse,
USFWS)



The arctic fox, a complex animal that has adapted to its environment, illustrates the relationships between an animal's form and function. The multicellular bodies of animals consist of tissues that make up more

complex organs and organ systems. The organ systems of an animal maintain homeostasis within the multicellular body. These systems are adapted to obtain the necessary nutrients and other resources needed by the cells of the body, to remove the wastes those cells produce, to coordinate the activities of the cells, tissues, and organs throughout the body, and to coordinate the many responses of the individual organism to its environment.

Homeostasis and Osmoregulation

By the end of this section, you will be able to:

- Explain the concept of homeostasis
- Describe thermoregulation of endothermic and ectothermic animals
- Explain how the kidneys serve as the main osmoregulatory organs in the human body

Homeostasis refers to the relatively stable state inside the body of an animal. Animal organs and organ systems constantly adjust to internal and external changes in order to maintain this steady state. Examples of internal conditions maintained homeostatically are the level of blood glucose, body temperature, blood calcium level. These conditions remain stable because of physiologic processes that result in negative feedback relationships. If the blood glucose or calcium rises, this sends a signal to organs responsible for lowering blood glucose or calcium. The signals that restore the normal levels are examples of negative feedback. When homeostatic mechanisms fail, the results can be unfavorable for the animal. Homeostatic mechanisms keep the body in dynamic equilibrium by constantly adjusting to the changes that the body's systems encounter. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium. Two examples of factors that are regulated homeostatically are temperature and water content. The processes that maintain homeostasis of these two factors are called thermoregulation and osmoregulation.

Homeostasis

The goal of homeostasis is the maintenance of equilibrium around a specific value of some aspect of the body or its cells called a **set point**. While there are normal fluctuations from the set point, the body's systems will usually attempt to go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the activities of the system so the value moves back toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If glucose levels in the blood rise after a meal, adjustments are made to lower them and to get the nutrient into tissues that need it or to store it for later use.

When a change occurs in an animal's environment, an adjustment must be made so that the internal environment of the body and cells remains stable. The receptor that senses the change in the environment is part of a feedback mechanism. The stimulus—temperature, glucose, or calcium levels—is detected by the receptor. The receptor sends information to a control center, often the brain, which relays appropriate signals to an effector organ that is able to cause an appropriate change, either up or down, depending on the information the sensor was sending.

Thermoregulation

Animals can be divided into two groups: those that maintain a constant body temperature in the face of differing environmental temperatures, and those that have a body temperature that is the same as their environment and thus varies with the environmental temperature. Animals that do not have internal control of their body temperature are called **ectotherms**. The body temperature of these organisms is generally similar to the temperature of the environment, although the individual organisms may do things that keep their bodies slightly below or above the environmental temperature. This can include burrowing underground on a hot day or resting in the sunlight on a cold day. The ectotherms have been called cold-blooded, a term that may not apply to an animal in the desert with a very warm body temperature.

An animal that maintains a constant body temperature in the face of environmental changes is called an **endotherm**. These animals are able to maintain a level of activity that an ectothermic animal cannot because they generate internal heat that keeps their cellular processes operating optimally even when the environment is cold.

Note:

Concept in Action



Watch this [Discovery Channel video](#) on thermoregulation to see illustrations of the process in a variety of animals.

Animals conserve or dissipate heat in a variety of ways. Endothermic animals have some form of insulation. They have fur, fat, or feathers. Animals with thick fur or feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals can increase body heat production by shivering, which is an involuntary increase in muscle activity. In addition, arrector pili muscles can contract causing individual hairs to stand up when the individual is cold. This increases the insulating effect of the hair. Humans retain this reaction, which does not have the intended effect on our relatively hairless bodies; it causes “goose bumps” instead. Mammals use layers of fat as insulation also. Loss of significant amounts of body fat will compromise an individual’s ability to conserve heat.

Ectotherms and endotherms use their circulatory systems to help maintain body temperature. Vasodilation, the opening up of arteries to the skin by relaxation of their smooth muscles, brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, cooling the body. Vasoconstriction, the narrowing of blood vessels to the skin by contraction of their smooth muscles, reduces blood flow in peripheral blood vessels, forcing blood toward the core and vital organs, conserving heat. Some animals have adaptations to their circulatory system that enable them to transfer heat from arteries to veins that are flowing next to each other, warming blood returning to the heart. This is called a countercurrent heat

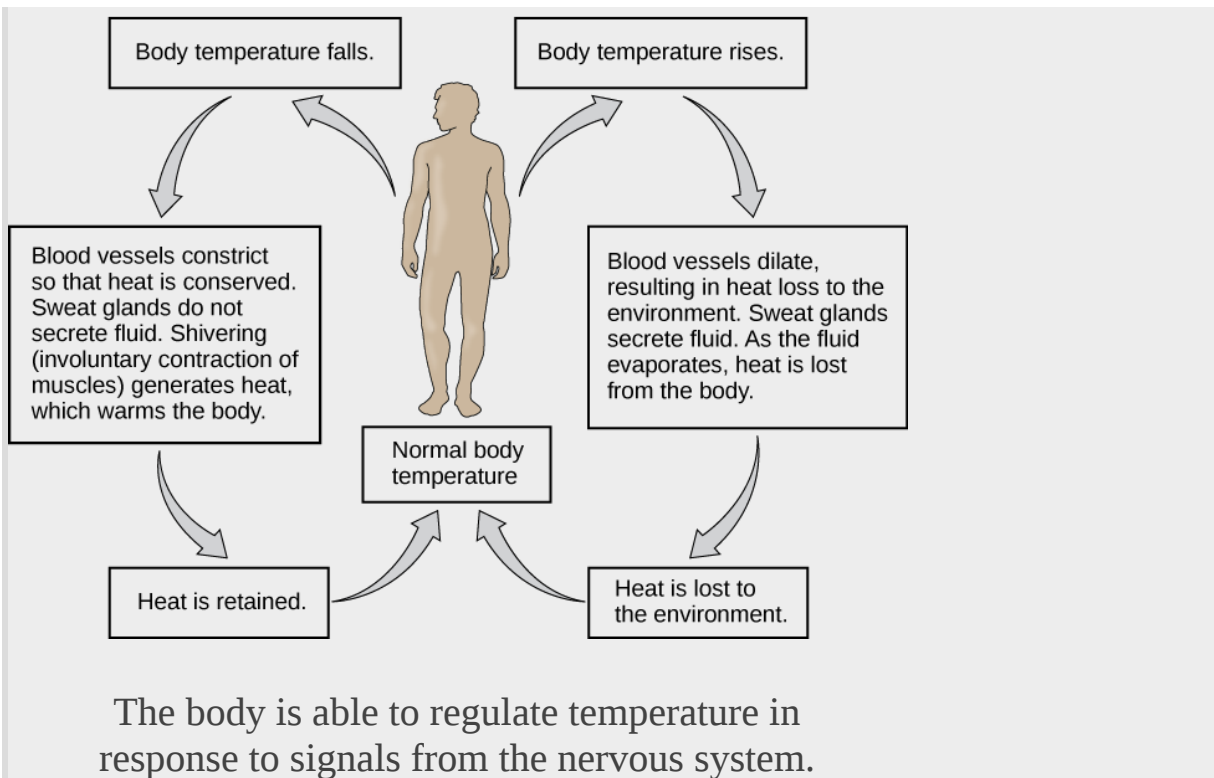
exchange; it prevents the cold venous blood from cooling the heart and other internal organs. The countercurrent adaptation is found in dolphins, sharks, bony fish, bees, and hummingbirds.

Some ectothermic animals use changes in their behavior to help regulate body temperature. They simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks in the evening to capture heat on a cold desert night before entering their burrows.

Thermoregulation is coordinated by the nervous system ([\[link\]](#)). The processes of temperature control are centered in the hypothalamus of the advanced animal brain. The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation or vasoconstriction and shivering or sweating. The sympathetic nervous system under control of the hypothalamus directs the responses that effect the changes in temperature loss or gain that return the body to the set point. The set point may be adjusted in some instances. During an infection, compounds called pyrogens are produced and circulate to the hypothalamus resetting the thermostat to a higher value. This allows the body's temperature to increase to a new homeostatic equilibrium point in what is commonly called a fever. The increase in body heat makes the body less optimal for bacterial growth and increases the activities of cells so they are better able to fight the infection.

Note:

Art Connection



When bacteria are destroyed by leukocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Osmoregulation

Osmoregulation is the process of maintaining salt and water balance (**osmotic balance**) across membranes within the body. The fluids inside and surrounding cells are composed of water, electrolytes, and nonelectrolytes. An electrolyte is a compound that dissociates into ions when dissolved in water. A nonelectrolyte, in contrast, does not dissociate into ions in water. The body's fluids include blood plasma, fluid that exists within cells, and the **interstitial fluid** that exists in the spaces between cells and tissues of the body. The membranes of the body (both the membranes around cells and the "membranes" made of cells lining body cavities) are semipermeable membranes. Semipermeable membranes are permeable to certain types of

solutes and to water, but typically cell membranes are impermeable to solutes.

The body does not exist in isolation. There is a constant input of water and electrolytes into the system. Excess water, electrolytes, and wastes are transported to the kidneys and excreted, helping to maintain osmotic balance. Insufficient fluid intake results in fluid conservation by the kidneys. Biological systems constantly interact and exchange water and nutrients with the environment by way of consumption of food and water and through excretion in the form of sweat, urine, and feces. Without a mechanism to regulate osmotic pressure, or when a disease damages this mechanism, there is a tendency to accumulate toxic waste and water, which can have dire consequences.

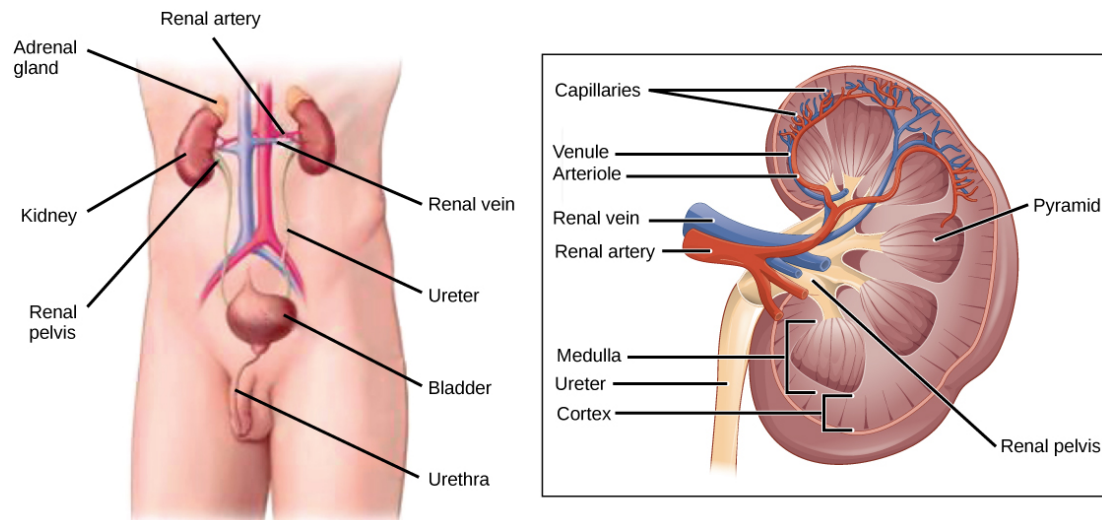
Mammalian systems have evolved to regulate not only the overall osmotic pressure across membranes, but also specific concentrations of important electrolytes in the three major fluid compartments: blood plasma, interstitial fluid, and intracellular fluid. Since osmotic pressure is regulated by the movement of water across membranes, the volume of the fluid compartments can also change temporarily. Since blood plasma is one of the fluid components, osmotic pressures have a direct bearing on blood pressure.

Excretory System

The human excretory system functions to remove waste from the body through the skin as sweat, the lungs in the form of exhaled carbon dioxide, and through the urinary system in the form of urine. All three of these systems participate in osmoregulation and waste removal. Here we focus on the urinary system, which is comprised of the paired kidneys, the ureter, urinary bladder and urethra ([\[link\]](#)). The **kidneys** are a pair of bean-shaped structures that are located just below the liver in the body cavity. Each of the kidneys contains more than a million tiny units called nephrons that filter blood containing the metabolic wastes from cells. All the blood in the human body is filtered about 60 times a day by the kidneys. The nephrons

remove wastes, concentrate them, and form urine that is collected in the bladder.

Internally, the kidney has three regions—an outer cortex, a medulla in the middle, and the renal pelvis, which is the expanded end of the ureter. The renal cortex contains the **nephrons**—the functional unit of the kidney. The renal pelvis collects the urine and leads to the **ureter** on the outside of the kidney. The ureters are urine-bearing tubes that exit the kidney and empty into the **urinary bladder**.



The human excretory system is made up of the kidneys, ureter, urinary bladder, and urethra. The kidneys filter blood and form urine, which is stored in the bladder until it is eliminated through the urethra. On the right, the internal structure of the kidney is shown. (credit: modification of work by NCI, NIH)

Blood enters each kidney from the aorta, the main artery supplying the body below the heart, through a **renal artery**. It is distributed in smaller vessels until it reaches each nephron in capillaries. Within the nephron the blood comes in intimate contact with the waste-collecting tubules in a structure called the glomerulus. Water and many solutes present in the blood,

including ions of sodium, calcium, magnesium, and others; as well as wastes and valuable substances such as amino acids, glucose and vitamins, leave the blood and enter the tubule system of the nephron. As materials pass through the tubule much of the water, required ions, and useful compounds are reabsorbed back into the capillaries that surround the tubules leaving the wastes behind. Some of this reabsorption requires active transport and consumes ATP. Some wastes, including ions and some drugs remaining in the blood, diffuse out of the capillaries into the interstitial fluid and are taken up by the tubule cells. These wastes are then actively secreted into the tubules. The blood then collects in larger and larger vessels and leaves the kidney in the renal vein. The **renal vein** joins the inferior vena cava, the main vein that returns blood to the heart from the lower body. The amounts of water and ions reabsorbed into the circulatory system are carefully regulated and this is an important way the body regulates its water content and ion levels. The waste is collected in larger tubules and then leaves the kidney in the ureter, which leads to the bladder where urine, the combination of waste materials and water, is stored.

The bladder contains sensory nerves, stretch receptors that signal when it needs to be emptied. These signals create the urge to urinate, which can be voluntarily suppressed up to a limit. The conscious decision to urinate sets in play signals that open the sphincters, rings of smooth muscle that close off the opening, to the **urethra** that allows urine to flow out of the bladder and the body.

Note:**Career in Action****Dialysis Technician**

Dialysis is a medical process of removing wastes and excess water from the blood by diffusion and ultrafiltration. When kidney function fails, dialysis must be done to artificially rid the body of wastes and fluids. This is a vital process to keep patients alive. In some cases, the patients undergo artificial dialysis until they are eligible for a kidney transplant. In others who are not candidates for kidney transplants, dialysis is a lifelong necessity.

Dialysis technicians typically work in hospitals and clinics. While some roles in this field include equipment development and maintenance, most dialysis technicians work in direct patient care. Their on-the-job duties, which typically occur under the direct supervision of a registered nurse, focus on providing dialysis treatments. This can include reviewing patient history and current condition, assessing and responding to patient needs before and during treatment, and monitoring the dialysis process. Treatment may include taking and reporting a patient's vital signs, preparing solutions and equipment to ensure accurate and sterile procedures.

Section Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is an equilibrium because body functions are kept within a normal range, with some fluctuations around a set point. The kidneys are the main osmoregulatory organs in mammalian systems; they function to filter blood and maintain the dissolved ion concentrations of body fluids. They are made up internally of three distinct regions—the cortex, medulla, and pelvis. The blood vessels that transport blood into and out of the kidneys arise from and merge with the aorta and inferior vena cava, respectively. The nephron is the functional unit of the kidney, which actively filters blood and generates urine. The urine leaves the kidney through the ureter and is stored in the urinary bladder. Urine is voided from the body through the urethra.

Art Connections

Exercise:

Problem:

[\[link\]](#) When bacteria are destroyed by leukocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

Solution:

[\[link\]](#) Pyrogens increase body temperature by causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.

Review Questions

Exercise:**Problem:**

When faced with a sudden drop in environmental temperature, an endothermic animal will _____.

- a. experience a drop in its body temperature
- b. wait to see if it goes lower
- c. increase muscle activity to generate heat
- d. add fur or fat to increase insulation

Solution:

C

Exercise:

Problem:How are wastes carried to the kidney for removal?

- a. in cells
- b. in the urine

- c. in blood
 - d. in interstitial fluid
-

Solution:

C

Exercise:

Problem: What is the cause of a fever of 38.3 °C (101 °F)?

- a. too much heat produced by the body
 - b. upward adjustment of the body temperature set point
 - c. inadequate cooling mechanisms in the body
 - d. the heat caused by a viral or bacterial infection
-

Solution:

B

Free Response

Exercise:

Problem: Describe how the body's mechanisms maintain homeostasis?

Solution:

The body has a sensor that detects a deviation of the state of the cells or the body from the set point. The information is relayed to a control center, usually the brain, where signals go to effectors. Those effectors cause a negative feedback response that moves the state of the body in a direction back toward the set point.

Exercise:

Problem:

Why is excretion important in order to achieve osmotic balance?

Solution:

Excretion allows an organism to rid itself of waste molecules that could be toxic if allowed to accumulate. It also allows the organism to keep the amount of water and dissolved solutes in balance.

Glossary

ectotherm

an organism that relies primarily on environmental heat sources to maintain its body temperature

endotherm

an organism that relies primarily on internal heat sources to maintain its body temperature

interstitial fluid

the fluid found between cells in the body, similar in constitution to the fluid component of blood, but without the high concentrations of proteins

kidney

the organ that performs excretory and osmoregulatory functions

nephron

the functional unit of the kidney

osmoregulation

the mechanism by which water and solute concentrations are maintained at desired levels

osmotic balance

the appropriate values of water and solute concentrations for a healthy organism

renal artery

the artery that delivers blood to the kidney

renal vein

the vein that drains blood from the kidney

set point

the target value of a physiological state in homeostasis

ureter

the urine-bearing tubes coming out of the kidney

urethra

the tube that conducts urine from the urinary bladder to the external environment

urinary bladder

the structure that the ureters empty the urine into

Digestive System

By the end of this section, you will be able to:

- Explain the processes of digestion and absorption
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients
- Describe the essential nutrients required for cellular function that cannot be synthesized by the animal body
- Describe how excess carbohydrates and energy are stored in the body

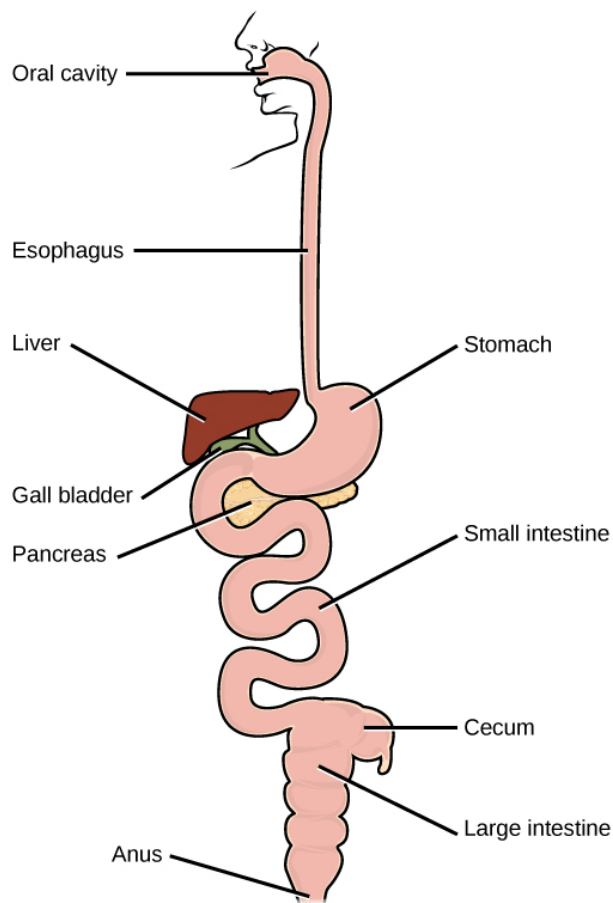
All living organisms need nutrients to survive. While plants can obtain nutrients from their roots and the energy molecules required for cellular function through the process of photosynthesis, animals obtain their nutrients by the consumption of other organisms. At the cellular level, the biological molecules necessary for animal function are amino acids, lipid molecules, nucleotides, and simple sugars. However, the food consumed consists of protein, fat, and complex carbohydrates. Animals must convert these macromolecules into the simple molecules required for maintaining cellular function. The conversion of the food consumed to the nutrients required is a multistep process involving digestion and absorption. During digestion, food particles are broken down to smaller components, which are later absorbed by the body. This happens by both physical means, such as chewing, and by chemical means.

One of the challenges in human nutrition is maintaining a balance between food intake, storage, and energy expenditure. Taking in more food energy than is used in activity leads to storage of the excess in the form of fat deposits. The rise in obesity and the resulting diseases like type 2 diabetes makes understanding the role of diet and nutrition in maintaining good health all the more important.

The Human Digestive System

The process of digestion begins in the mouth with the intake of food ([link](#)). The teeth play an important role in masticating (chewing) or

physically breaking food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The food is then swallowed and enters the **esophagus**—a long tube that connects the mouth to the stomach. Using **peristalsis**, or wave-like smooth-muscle contractions, the muscles of the esophagus push the food toward the stomach. The stomach contents are extremely acidic, with a pH between 1.5 and 2.5. This acidity kills microorganisms, breaks down food tissues, and activates digestive enzymes. Further breakdown of food takes place in the small intestine where bile produced by the liver, and enzymes produced by the small intestine and the pancreas, continue the process of digestion. The smaller molecules are absorbed into the blood stream through the epithelial cells lining the walls of the small intestine. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the anus.

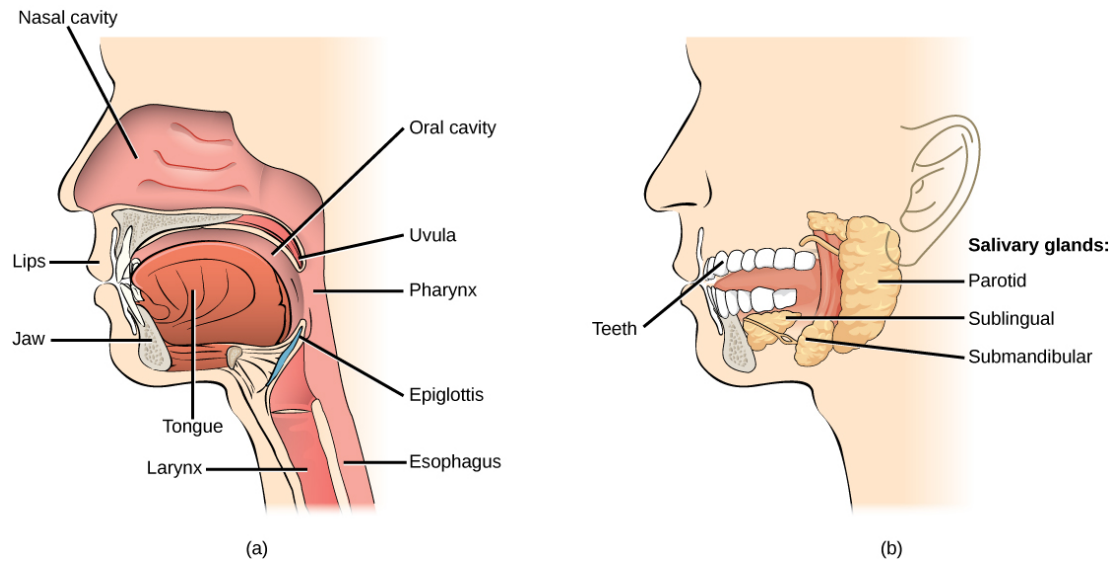


The components of the human digestive system are shown.

Oral Cavity

Both physical and chemical digestion begin in the mouth or **oral cavity**, which is the point of entry of food into the digestive system. The food is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food to begin the process of physically breaking it down into smaller particles.

The chemical process of digestion begins during chewing as food mixes with saliva, produced by the **salivary glands** ([link](#)). Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains lysozyme, which has antibacterial action. It also contains an enzyme called salivary **amylase** that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called lipase is produced by cells in the tongue to break down fats. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the **bolus** for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the esophagus and the trachea. The esophagus leads to the stomach and the trachea leads to the lungs. The epiglottis is a flap of tissue that covers the tracheal opening during swallowing to prevent food from entering the lungs.



(a) Digestion of food begins in the mouth. (b) Food is masticated by teeth and moistened by saliva secreted from the salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by Mariana Ruiz Villareal)

Esophagus

The esophagus is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo peristalsis that pushes the food toward the stomach. The peristaltic wave is unidirectional—it moves food from the mouth the stomach, and reverse movement is not possible, except in the case of the vomit reflex. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

Ring-like muscles called sphincters form valves in the digestive system. The gastro-esophageal sphincter (or cardiac sphincter) is located at the

stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Acid reflux or “heartburn” occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of protein digestion occurs in the stomach ([link](#)). The **stomach** is a saclike organ that secretes gastric digestive juices.

Protein digestion is carried out by an enzyme called **pepsin** in the stomach chamber. The highly acidic environment kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the catabolism of protein in the food. Chemical digestion is facilitated by the churning action of the stomach caused by contraction and relaxation of smooth muscles. The partially digested food and gastric juice mixture is called **chyme**. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by hormones, stomach distension and muscular reflexes that influence the pyloric sphincter.

The stomach lining is unaffected by pepsin and the acidity because pepsin is released in an inactive form and the stomach has a thick mucus lining that protects the underlying tissue.

Small Intestine

Chyme moves from the stomach to the small intestine. The **small intestine** is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the villi. The top

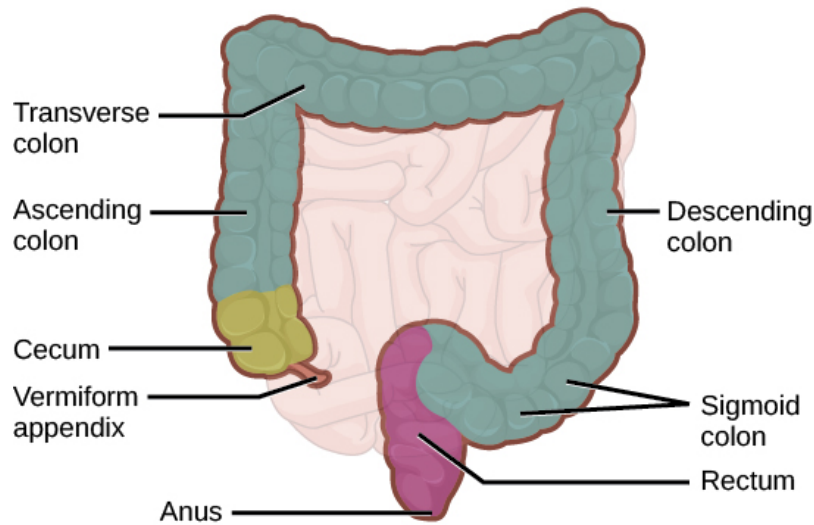
surface of each villus has many microscopic projections called microvilli. The epithelial cells of these structures absorb nutrients from the digested food and release them to the bloodstream on the other side. The villi and microvilli, with their many folds, increase the surface area of the small intestine and increase absorption efficiency of the nutrients.

The human small intestine is over 6 m (19.6 ft) long and is divided into three parts: the duodenum, the jejunum and the ileum. The duodenum is separated from the stomach by the pyloric sphincter. The chyme is mixed with pancreatic juices, an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme from the stomach. Pancreatic juices contain several digestive enzymes that break down starches, disaccharides, proteins, and fats. **Bile** is produced in the liver and stored and concentrated in the gallbladder; it enters the duodenum through the bile duct. Bile contains bile salts, which make lipids accessible to the water-soluble enzymes. The monosaccharides, amino acids, bile salts, vitamins, and other nutrients are absorbed by the cells of the intestinal lining.

The undigested food is sent to the colon from the ileum via peristaltic movements. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, “worm-like,” appendix is located at the ileocecal valve. The appendix of humans has a minor role in immunity.

Large Intestine

The **large intestine** reabsorbs the water from indigestible food material and processes the waste material ([\[link\]](#)). The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or “intestinal flora” that aid in the digestive processes. The **colon** has four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material.



The large intestine reabsorbs water from undigested food and stores waste until it is eliminated. (credit: modification of work by Mariana Ruiz Villareal)

The **rectum** ([link](#)) stores feces until defecation. The feces are propelled using peristaltic movements during elimination. The **anus** is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters regulate the exit of feces, the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

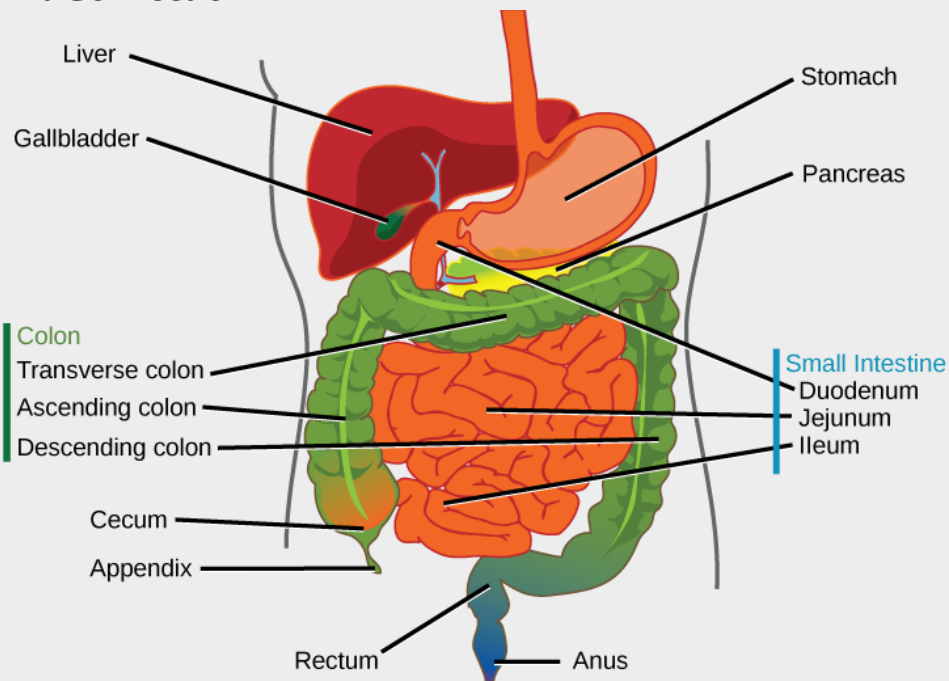
The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs add secretions and enzymes that break down food into nutrients. Accessory organs include the salivary glands, the liver, the pancreas, and the gall bladder. The secretions of the liver, pancreas, and gallbladder are regulated by hormones in response to food consumption.

The **liver** is the largest internal organ in humans and it plays an important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fats in the duodenum. The liver also processes the absorbed vitamins and fatty acids and synthesizes many plasma proteins. The **gallbladder** is a small organ that aids the liver by storing bile and concentrating bile salts.

The **pancreas** secretes bicarbonate that neutralizes the acidic chyme and a variety of enzymes for the digestion of protein and carbohydrates.

Note:

Art Connection



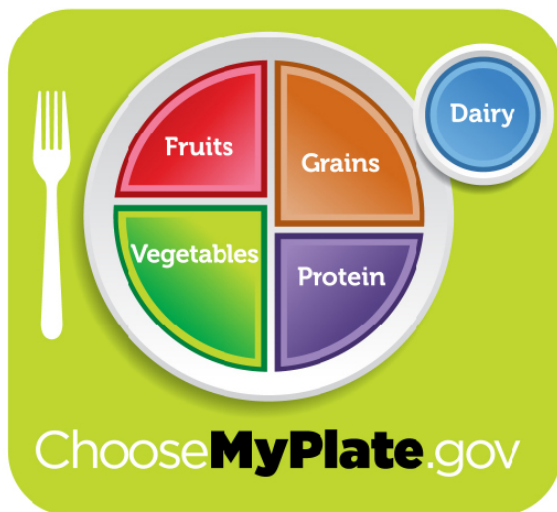
The stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)

Which of the following statements about the digestive system is false?

- a. Chyme is a mixture of food and digestive juices that is produced in the stomach.
- b. Food enters the large intestine before the small intestine.
- c. In the small intestine, chyme mixes with bile, which emulsifies fats.
- d. The stomach is separated from the small intestine by the pyloric sphincter.

Nutrition

The human diet should be well balanced to provide nutrients required for bodily function and the minerals and vitamins required for maintaining structure and regulation necessary for good health and reproductive capability ([\[link\]](#)).



For humans, a balanced diet includes fruits, vegetables, grains, protein, and dairy.
(credit: USDA)

Note:

Concept in Action



Explore this [interactive United States Department of Agriculture website](#) to learn more about each food group and the recommended daily amounts.

The organic molecules required for building cellular material and tissues must come from food. During digestion, digestible carbohydrates are ultimately broken down into glucose and used to provide energy within the cells of the body. Complex carbohydrates, including polysaccharides, can be broken down into glucose through biochemical modification; however, humans do not produce the enzyme necessary to digest cellulose (fiber). The intestinal flora in the human gut are able to extract some nutrition from these plant fibers. These plant fibers are known as dietary fiber and are an important component of the diet. The excess sugars in the body are converted into glycogen and stored for later use in the liver and muscle tissue. Glycogen stores are used to fuel prolonged exertions, such as long-distance running, and to provide energy during food shortage. Fats are stored under the skin of mammals for insulation and energy reserves.

Proteins in food are broken down during digestion and the resulting amino acids are absorbed. All of the proteins in the body must be formed from these amino-acid constituents; no proteins are obtained directly from food.

Fats add flavor to food and promote a sense of satiety or fullness. Fatty foods are also significant sources of energy, and fatty acids are required for the construction of lipid membranes. Fats are also required in the diet to aid the absorption of fat-soluble vitamins and the production of fat-soluble hormones.

While the animal body can synthesize many of the molecules required for function from precursors, there are some nutrients that must be obtained from food. These nutrients are termed **essential nutrients**, meaning they must be eaten, because the body cannot produce them.

The fatty acids omega-3 alpha-linolenic acid and omega-6 linoleic acid are essential fatty acids needed to make some membrane phospholipids.

Vitamins are another class of essential organic molecules that are required in small quantities. Many of these assist enzymes in their function and, for this reason, are called coenzymes. Absence or low levels of vitamins can have a dramatic effect on health. **Minerals** are another set of inorganic essential nutrients that must be obtained from food. Minerals perform many functions, from muscle and nerve function, to acting as enzyme cofactors. Certain amino acids also must be procured from food and cannot be synthesized by the body. These amino acids are the “essential” amino acids. The human body can synthesize only 11 of the 20 required amino acids; the rest must be obtained from food.

Note:

Biology in action

Obesity

With obesity at high rates in the United States, there is a public health focus on reducing obesity and associated health risks, which include diabetes, colon and breast cancer, and cardiovascular disease. How does the food consumed contribute to obesity?

Fatty foods are calorie-dense, meaning that they have more calories per unit mass than carbohydrates or proteins. One gram of carbohydrates has four calories, one gram of protein has four calories, and one gram of fat has nine calories. Animals tend to seek lipid-rich food for their higher energy content. Greater amounts of food energy taken in than the body's requirements will result in storage of the excess in fat deposits.

Excess carbohydrate is used by the liver to synthesize glycogen. When glycogen stores are full, additional glucose is converted into fatty acids. These fatty acids are stored in adipose tissue cells—the fat cells in the mammalian body whose primary role is to store fat for later use.

The rate of obesity among children is rapidly rising in the United States. To combat childhood obesity and ensure that children get a healthy start in life, in 2010 First Lady Michelle Obama launched the Let's Move! campaign. The goal of this campaign is to educate parents and caregivers on providing healthy nutrition and encouraging active lifestyles in future generations. This program aims to involve the entire community, including parents, teachers, and healthcare providers to ensure that children have access to healthy foods—more fruits, vegetables, and whole grains—and consume fewer calories from processed foods. Another goal is to ensure that children get physical activity. With the increase in television viewing and stationary pursuits such as video games, sedentary lifestyles have become the norm. Visit www.letsmove.gov to learn more.

Section Summary

There are many organs that work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. The enzyme pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Carbohydrates, proteins, and fats are the primary components of food. Some essential nutrients are required for cellular function but cannot be produced by the animal body. These include vitamins, minerals, some fatty acids, and some amino acids. Food intake in more than necessary amounts is stored as glycogen in the liver and muscle cells, and in adipose tissue. Excess adipose storage can lead to obesity and serious health problems.

Art Connections

Exercise:

Problem:

[\[link\]](#) Which of the following statements about the digestive system is false?

- a. Chyme is a mixture of food and digestive juices that is produced in the stomach.
- b. Food enters the large intestine before the small intestine.
- c. In the small intestine, chyme mixes with bile, which emulsifies fats.
- d. The stomach is separated from the small intestine by the pyloric sphincter.

Solution:

[\[link\]](#) B

Review Questions**Exercise:**

Problem:Where does the majority of fat digestion take place?

- a. mouth
- b. stomach
- c. small intestine
- d. large intestine

Solution:

C

Exercise:

Problem:The bile from the liver is delivered to the _____.

- a. stomach
- b. liver
- c. small intestine
- d. colon

Solution:

C

Exercise:

Problem: Which of the following statements is not true?

- a. Essential nutrients can be synthesized by the body.
- b. Vitamins are required in small quantities for bodily function.
- c. Some amino acids can be synthesized by the body, while others need to be obtained from diet.
- d. Vitamins come in two categories: fat-soluble and water-soluble.

Solution:

A

Free Response

Exercise:

Problem: What is the role of the accessory organs in digestion?

Solution:

Accessory organs play an important role in producing and delivering digestive juices to the intestine during digestion and absorption. Specifically, the salivary glands, liver, pancreas, and gallbladder play

important roles. Malfunction of any of these organs can lead to disease states.

Exercise:

Problem:What is the role of minerals in maintaining good health?

Solution:

Minerals—such as potassium, sodium, and calcium—are required for the functioning of many cellular processes. While minerals are required in trace amounts, not having minerals in the diet can be potentially harmful.

Exercise:

Problem:Discuss why obesity is a growing epidemic.

Solution:

In the United States, obesity, particularly childhood obesity, is a growing concern. Some of the contributors to this situation include sedentary lifestyles and consuming more processed foods and less fruits and vegetables. As a result, even young children who are obese can face health concerns.

Glossary

amylase

an enzyme found in saliva and secreted by the pancreas that converts carbohydrates to maltose

anus

the exit point of the digestive system for waste material

bile

a digestive juice produced by the liver; important for digestion of lipids

bolus

a mass of food resulting from chewing action and wetting by saliva

colon

the largest portion of the large intestine consisting of the ascending colon, transverse colon, and descending colon

chyme

a mixture of partially digested food and stomach juices

esophagus

a tubular organ that connects the mouth to the stomach

essential nutrient

a nutrient that cannot be synthesized by the body; it must be obtained from food

gallbladder

the organ that stores and concentrates bile

large intestine

a digestive system organ that reabsorbs water from undigested material and processes waste matter

liver

an organ that produces bile for digestion and processes vitamins and lipids

mineral

an inorganic, elemental molecule that carries out important roles in the body

oral cavity

the point of entry of food into the digestive system

pancreas

a gland that secretes digestive juices

pepsin

an enzyme found in the stomach whose main role is protein digestion

peristalsis

wave-like movements of muscle tissue

rectum

the area of the body where feces is stored until elimination

salivary gland

one of three pairs of exocrine glands in the mammalian mouth that secretes saliva, a mix of watery mucus and enzymes

small intestine

the organ where digestion of protein, fats, and carbohydrates is completed

stomach

a saclike organ containing acidic digestive juices

vitamin

an organic substance necessary in small amounts to sustain life

Circulatory and Respiratory Systems

By the end of this section, you will be able to:

- Describe the passage of air from the outside environment to the lungs
- Describe the function of the circulatory system
- Describe the cardiac cycle
- Explain how blood flows through the body

Animals are complex multicellular organisms that require a mechanism for transporting nutrients throughout their bodies and removing wastes. The human circulatory system has a complex network of blood vessels that reach all parts of the body. This extensive network supplies the cells, tissues, and organs with oxygen and nutrients, and removes carbon dioxide and waste compounds.

The medium for transport of gases and other molecules is the blood, which continually circulates through the system. Pressure differences within the system cause the movement of the blood and are created by the pumping of the heart.

Gas exchange between tissues and the blood is an essential function of the circulatory system. In humans, other mammals, and birds, blood absorbs oxygen and releases carbon dioxide in the lungs. Thus the circulatory and respiratory system, whose function is to obtain oxygen and discharge carbon dioxide, work in tandem.

The Respiratory System

Take a breath in and hold it. Wait several seconds and then let it out. Humans, when they are not exerting themselves, breathe approximately 15 times per minute on average. This equates to about 900 breaths an hour or 21,600 breaths per day. With every inhalation, air fills the lungs, and with every exhalation, it rushes back out. That air is doing more than just inflating and deflating the lungs in the chest cavity. The air contains oxygen that crosses the lung tissue, enters the bloodstream, and travels to organs and tissues. There, oxygen is exchanged for carbon dioxide, which is a cellular waste material. Carbon dioxide exits the cells, enters the

bloodstream, travels back to the lungs, and is expired out of the body during exhalation.

Breathing is both a voluntary and an involuntary event. How often a breath is taken and how much air is inhaled or exhaled is regulated by the respiratory center in the brain in response to signals it receives about the carbon dioxide content of the blood. However, it is possible to override this automatic regulation for activities such as speaking, singing and swimming under water.

During inhalation the **diaphragm** descends creating a negative pressure around the lungs and they begin to inflate, drawing in air from outside the body. The air enters the body through the **nasal cavity** located just inside the nose ([\[link\]](#)). As the air passes through the nasal cavity, the air is warmed to body temperature and humidified by moisture from mucous membranes. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages by hairs, mucus, and cilia. Air is also chemically sampled by the sense of smell.

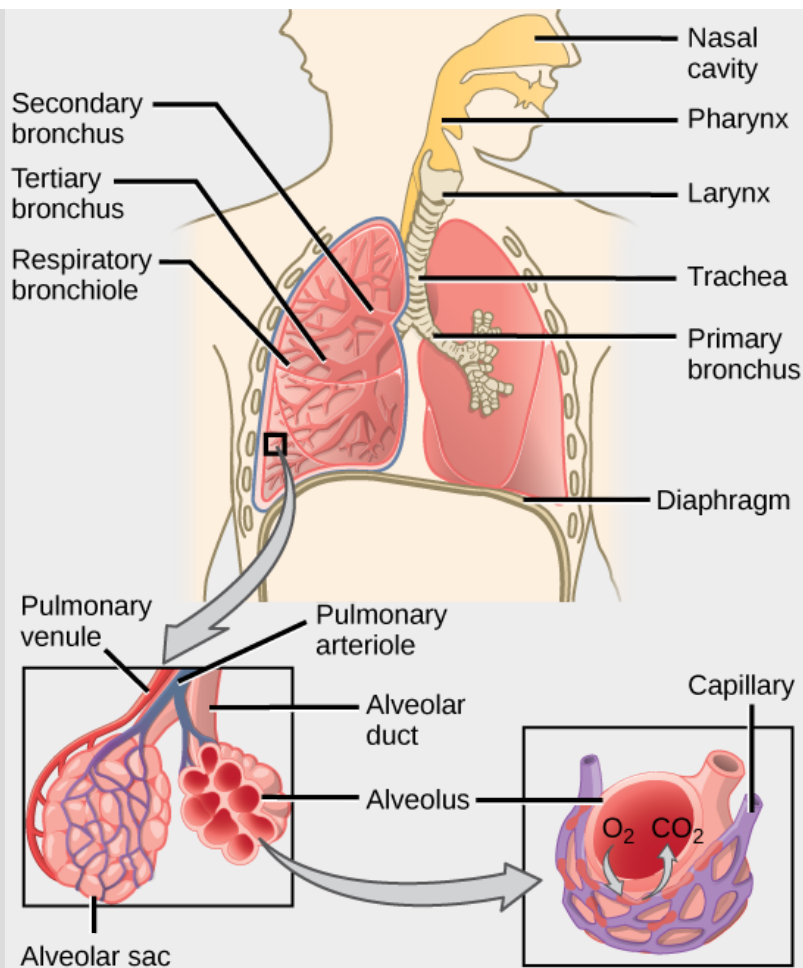
From the nasal cavity, air passes through the **pharynx** (throat) and the **larynx** (voice box) as it makes its way to the **trachea** ([\[link\]](#)). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder, about 25 to 30 cm (9.8–11.8 in) long, which sits in front of the esophagus and extends from the pharynx into the chest cavity to the lungs. It is made of incomplete rings of cartilage and smooth muscle. The cartilage provides strength and support to the trachea to keep the passage open. The trachea is lined with cells that have cilia and secrete mucus. The mucus catches particles that have been inhaled, and the cilia move the particles toward the pharynx.

The end of the trachea divides into two bronchi that enter the right and left lung. Air enters the lungs through the **primary bronchi**. The primary bronchus divides, creating smaller and smaller diameter **bronchi** until the passages are under 1 mm (.03 in) in diameter when they are called **bronchioles** as they split and spread through the lung. Like the trachea, the bronchus and bronchioles are made of cartilage and smooth muscle.

Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. The final bronchioles are the respiratory bronchioles. Alveolar ducts are attached to the end of each respiratory bronchiole. At the end of each duct are alveolar sacs, each containing 20 to 30 **alveoli**. Gas exchange occurs only in the alveoli. The alveoli are thin-walled and look like tiny bubbles within the sacs. The alveoli are in direct contact with capillaries of the circulatory system. Such intimate contact ensures that oxygen will diffuse from the alveoli into the blood. In addition, carbon dioxide will diffuse from the blood into the alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Estimates for the surface area of alveoli in the lungs vary around 100 m^2 . This large area is about the area of half a tennis court. This large surface area, combined with the thin-walled nature of the alveolar cells, allows gases to easily diffuse across the cells.

Note:

Art Connection



Air enters the respiratory system through the nasal cavity, and then passes through the pharynx and the trachea into the lungs.
(credit: modification of work by NCI)

Which of the following statements about the human respiratory system is false?

- When we breathe in, air travels from the pharynx to the trachea.
- The bronchioles branch into bronchi.
- Alveolar ducts connect to alveolar sacs.
- Gas exchange between the lungs and blood takes place in the alveolus.

Note:**Concept in Action**

Watch this [video](#) for a review of the respiratory system.

The Circulatory System

The circulatory system is a network of vessels—the arteries, veins, and capillaries—and a pump, the heart. In all vertebrate organisms this is a closed-loop system, in which the blood is largely separated from the body's other extracellular fluid compartment, the interstitial fluid, which is the fluid bathing the cells. Blood circulates inside blood vessels and circulates unidirectionally from the heart around one of two circulatory routes, then returns to the heart again; this is a **closed circulatory system**. **Open circulatory systems** are found in invertebrate animals in which the circulatory fluid bathes the internal organs directly even though it may be moved about with a pumping heart.

The Heart

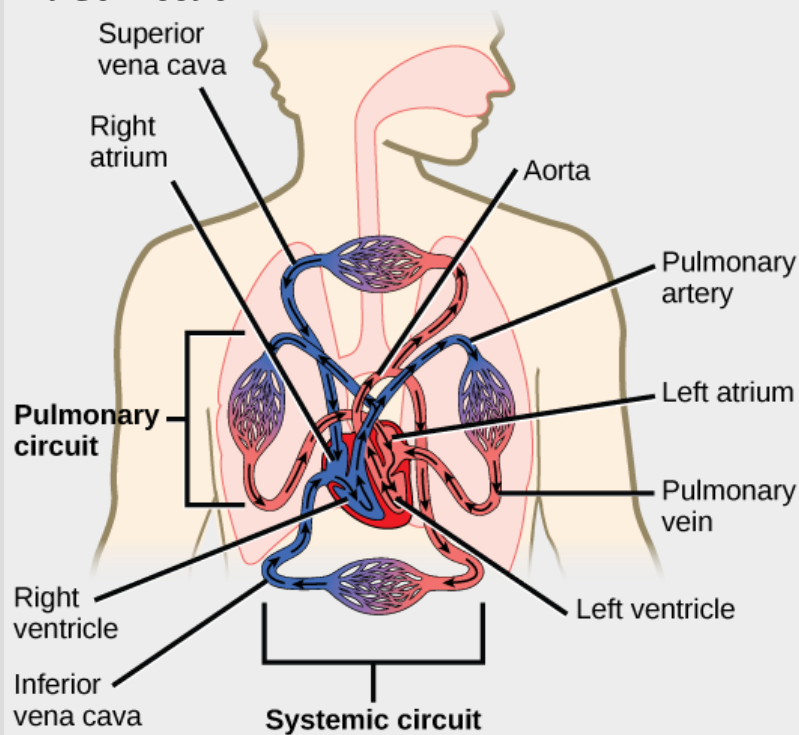
The heart is a complex muscle that consists of two pumps: one that pumps blood through **pulmonary circulation** to the lungs, and the other that pumps blood through **systemic circulation** to the rest of the body's tissues (and the heart itself).

The heart is asymmetrical, with the left side being larger than the right side, correlating with the different sizes of the pulmonary and systemic circuits ([link](#)). In humans, the heart is about the size of a clenched fist; it is divided into four chambers: two atria and two ventricles. There is one

atrium and one **ventricle** on the right side and one atrium and one ventricle on the left side. The right atrium receives deoxygenated blood from the systemic circulation through the major veins: the **superior vena cava**, which drains blood from the head and from the veins that come from the arms, as well as the **inferior vena cava**, which drains blood from the veins that come from the lower organs and the legs. This deoxygenated blood then passes to the right ventricle through the **tricuspid valve**, which prevents the backflow of blood. After it is filled, the right ventricle contracts, pumping the blood to the lungs for reoxygenation. The left atrium receives the oxygen-rich blood from the lungs. This blood passes through the **bicuspid valve** to the left ventricle where the blood is pumped into the **aorta**. The aorta is the major artery of the body, taking oxygenated blood to the organs and muscles of the body. This pattern of pumping is referred to as double circulation and is found in all mammals. ([link](#)).

Note:

Art Connection



The heart is divided into four chambers, two

atria, and two ventricles. Each chamber is separated by one-way valves. The right side of the heart receives deoxygenated blood from the body and pumps it to the lungs. The left side of the heart pumps blood to the rest of the body.

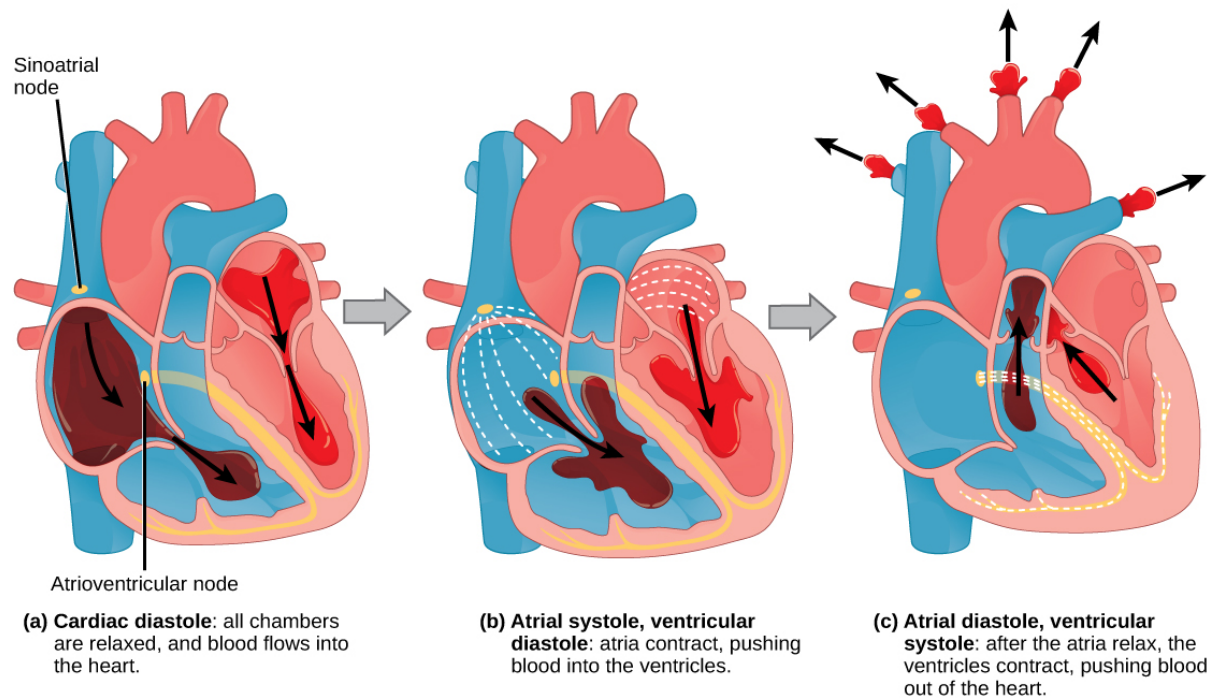
Which of the following statements about the circulatory system is false?

- a. Blood in the pulmonary vein is deoxygenated.
- b. Blood in the inferior vena cava is deoxygenated.
- c. Blood in the pulmonary artery is deoxygenated.
- d. Blood in the aorta is oxygenated.

The Cardiac Cycle

The main purpose of the heart is to pump blood through the body; it does so in a repeating sequence called the cardiac cycle. The **cardiac cycle** is the flow of blood through the heart coordinated by electrochemical signals that cause the heart muscle to contract and relax. In each cardiac cycle, a sequence of contractions pushes out the blood, pumping it through the body; this is followed by a relaxation phase, where the heart fills with blood. These two phases are called the **systole** (contraction) and **diastole** (relaxation), respectively ([link](#)). The signal for contraction begins at a location on the outside of the right atrium. The electrochemical signal moves from there across the atria causing them to contract. The contraction of the atria forces blood through the valves into the ventricles. Closing of these valves caused by the contraction of the ventricles produces a “lub” sound. The signal has, by this time, passed down the walls of the heart, through a point between the right atrium and right ventricle. The signal then causes the ventricles to contract. The ventricles contract together forcing blood into the aorta and the pulmonary arteries. Closing of the valves to

these arteries caused by blood being drawn back toward the heart during ventricular relaxation produces a monosyllabic “dub” sound.



In each cardiac cycle, a series of contractions (systoles) and relaxations (diastoles) pumps blood through the heart and through the body. (a) During cardiac diastole, blood flows into the heart while all chambers are relaxed. (b) Then the ventricles remain relaxed while atrial systole pushes blood into the ventricles. (c) Once the atria relax again, ventricle systole pushes blood out of the heart.

The pumping of the heart is a function of the cardiac muscle cells, or cardiomyocytes, that make up the heart muscle. Cardiomyocytes are distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle; adjacent cells are connected by intercalated disks found only in cardiac muscle. These connections allow the electrical signal to travel directly to neighboring muscle cells.

The electrical impulses in the heart produce electrical currents that flow through the body and can be measured on the skin using electrodes. This information can be observed as an **electrocardiogram (ECG)** a recording of the electrical impulses of the cardiac muscle.

Note:

Concept in Action



Visit the following [website](#) to see the heart's pacemaker, or electrocardiogram system, in action.

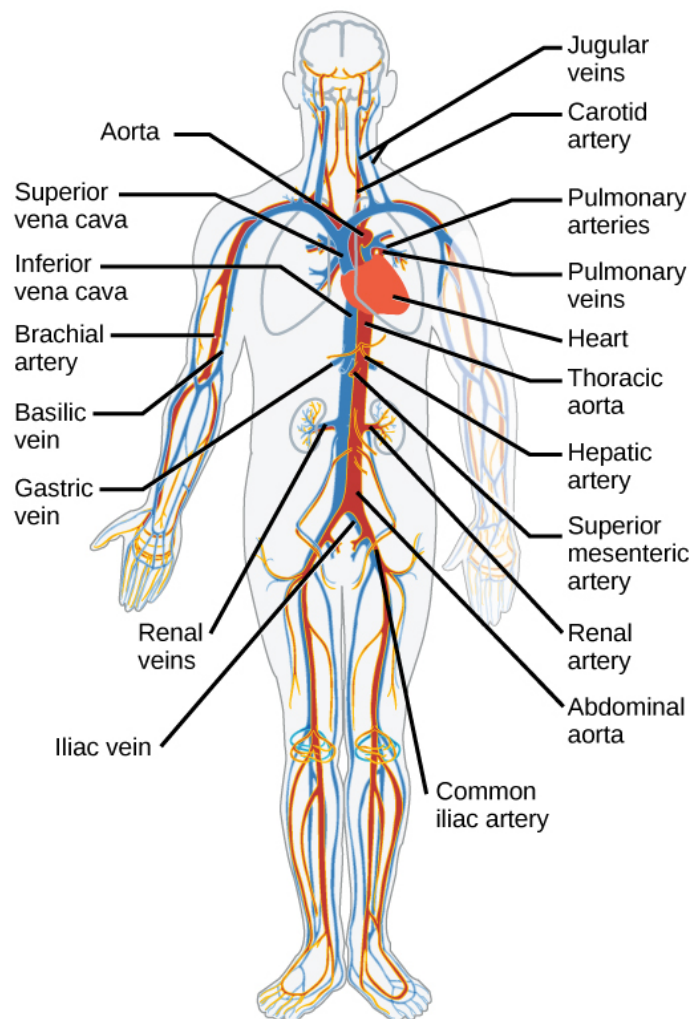
Blood Vessels

The blood from the heart is carried through the body by a complex network of blood vessels ([\[link\]](#)). **Arteries** take blood away from the heart. The main artery of the systemic circulation is the aorta; it branches into major arteries that take blood to different limbs and organs. The aorta and arteries near the heart have heavy but elastic walls that respond to and smooth out the pressure differences caused by the beating heart. Arteries farther away from the heart have more muscle tissue in their walls that can constrict to affect flow rates of blood. The major arteries diverge into minor arteries, and then smaller vessels called arterioles, to reach more deeply into the muscles and organs of the body.

Arterioles diverge into capillary beds. Capillary beds contain a large number, 10's to 100's of **capillaries** that branch among the cells of the body. Capillaries are narrow-diameter tubes that can fit single red blood cells and are the sites for the exchange of nutrients, waste, and oxygen with

tissues at the cellular level. Fluid also leaks from the blood into the interstitial space from the capillaries. The capillaries converge again into venules that connect to minor veins that finally connect to major veins.

Veins are blood vessels that bring blood high in carbon dioxide back to the heart. Veins are not as thick-walled as arteries, since pressure is lower, and they have valves along their length that prevent backflow of blood away from the heart. The major veins drain blood from the same organs and limbs that the major arteries supply.



The arteries of the body, indicated in red, start at the aortic arch and branch to supply the organs and

muscles of the body with oxygenated blood. The veins of the body, indicated in blue, return blood to the heart. The pulmonary arteries are blue to reflect the fact that they are deoxygenated, and the pulmonary veins are red to reflect that they are oxygenated. (credit: modification of work by Mariana Ruiz Villareal)

Section Summary

Animal respiratory systems are designed to facilitate gas exchange. In mammals, air is warmed and humidified in the nasal cavity. Air then travels down the pharynx and larynx, through the trachea, and into the lungs. In the lungs, air passes through the branching bronchi, reaching the respiratory bronchioles. The respiratory bronchioles open up into the alveolar ducts, alveolar sacs, and alveoli. Because there are so many alveoli and alveolar sacs in the lung, the surface area for gas exchange is very large.

The mammalian circulatory system is a closed system with double circulation passing through the lungs and the body. It consists of a network of vessels containing blood that circulates because of pressure differences generated by the heart.

The heart contains two pumps that move blood through the pulmonary and systemic circulations. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The pumping of the heart is a function of cardiomyocytes, distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle. The signal for contraction begins in the wall of the right atrium. The electrochemical signal causes the two atria to contract in unison; then the signal causes the ventricles to contract. The blood from the heart is carried through the body by a complex network of blood vessels;

arteries take blood away from the heart, and veins bring blood back to the heart.

Art Connections

Exercise:

Problem:

[\[link\]](#) Which of the following statements about the human respiratory system is false?

- a. When we breathe in, air travels from the pharynx to the trachea.
- b. The bronchioles branch into bronchi.
- c. Alveolar ducts connect to alveolar sacs.
- d. Gas exchange between the lungs and blood takes place in the alveolus.

Solution:

[\[link\]](#) B

Exercise:

Problem:

[\[link\]](#) Which of the following statements about the circulatory system is false?

- a. Blood in the pulmonary vein is deoxygenated.
- b. Blood in the inferior vena cava is deoxygenated.
- c. Blood in the pulmonary artery is deoxygenated.
- d. Blood in the aorta is oxygenated.

Solution:

[\[link\]](#) A

Review Questions

Exercise:

Problem: The respiratory system _____.

- a. provides body tissues with oxygen
- b. provides body tissues with oxygen and carbon dioxide
- c. establishes how many breaths are taken per minute
- d. provides the body with carbon dioxide

Solution:

A

Exercise:

Problem: Which is the order of airflow during inhalation?

- a. nasal cavity, trachea, larynx, bronchi, bronchioles, alveoli
- b. nasal cavity, larynx, trachea, bronchi, bronchioles, alveoli
- c. nasal cavity, larynx, trachea, bronchioles, bronchi, alveoli
- d. nasal cavity, trachea, larynx, bronchi, bronchioles, alveoli

Solution:

B

Exercise:

Problem: Where does the right ventricle send blood?

- a. the head
- b. the upper body
- c. the lungs
- d. the lower body

Solution:

C

Exercise:

Problem:

During the systolic phase of the cardiac cycle, the heart is _____.

- a. contracting
- b. relaxing
- c. contracting and relaxing
- d. filling with blood

Solution:

A

Exercise:

Problem:How do arteries differ from veins?

- a. Arteries have thicker wall layers to accommodate the changes in pressure from the heart.
- b. Arteries carry blood.
- c. Arteries have thinner wall layers and valves and move blood by the action of skeletal muscle.
- d. Arteries are thin walled and are used for gas exchange.

Solution:

A

Free Response

Exercise:**Problem:**

Describe the function of these terms and describe where they are located: main bronchus, trachea, alveoli.

Solution:

The main bronchus is the conduit in the lung that funnels air to the airways where gas exchange occurs. The main bronchus attaches the lungs to the very end of the trachea where it bifurcates. The trachea is the cartilaginous structure that extends from the pharynx to the lungs. It serves to funnel air to the lungs. The alveoli are the site of gas exchange; they are located at the terminal regions of the lung and are attached to the alveolar sacs, which come from the alveolar ducts and respiratory bronchioles terminal bronchi.

Exercise:

Problem: How does the structure of alveoli maximize gas exchange?

Solution:

The sac-like structure of the alveoli increases their surface area. In addition, the alveoli are made of thin-walled cells. These features allows gases to easily diffuse across the cells.

Exercise:

Problem: Describe the cardiac cycle.

Solution:

The heart receives an electrical signal triggering the cardiac muscle cells in the atria to contract. The signal pauses before passing onto the ventricles so the blood is pumped through the body. This is the systolic phase. The heart then relaxes in diastole and fills again with blood.

Glossary

alveolus

(plural: alveoli) (also, air sacs) the terminal structure of the lung passage where gas exchange occurs

aorta

the major artery that takes blood away from the heart to the systemic circulatory system

artery

a blood vessel that takes blood away from the heart

atrium

(plural: atria) a chamber of the heart that receives blood from the veins

bicuspid valve

a one-way opening between the atrium and the ventricle in the left side of the heart

bronchi

(singular: bronchus) smaller branches of cartilaginous tissue that stem off of the trachea; air is funneled through the bronchi to the region where gas exchange occurs in the alveoli

bronchiole

an airway that extends from the main bronchus to the alveolar sac

capillary

the smallest blood vessel that allows the passage of individual blood cells and the site of diffusion of oxygen and nutrient exchange

cardiac cycle

the filling and emptying the heart of blood caused by electrical signals that cause the heart muscles to contract and relax

closed circulatory system

a system that has the blood separated from the bodily interstitial fluid and contained in blood vessels

diaphragm

a skeletal muscle located under lungs that encloses the lungs in the thorax

diastole

the relaxation phase of the cardiac cycle when the heart is relaxed and the ventricles are filling with blood

electrocardiogram (ECG)

a recording of the electrical impulses of the cardiac muscle

inferior vena cava

the major vein of the body returning blood from the lower parts of the body to the right atrium

larynx

the voice box, located within the throat

nasal cavity

an opening of the respiratory system to the outside environment

open circulatory system

a circulatory system that has the blood mixed with interstitial fluid in the body cavity and directly bathes the organs

pharynx

the throat

primary bronchus

(also, main bronchus) a region of the airway within the lung that attaches to the trachea and bifurcates to form the bronchioles

pulmonary circulation

the flow of blood away from the heart through the lungs where oxygenation occurs and then back to the heart

superior vena cava

the major vein of the body returning blood from the upper part of the body to the right atrium

systemic circulation

the flow of blood away from the heart to the brain, liver, kidneys, stomach, and other organs, the limbs, and the muscles of the body, and then back to the heart

systole

the contraction phase of cardiac cycle when the ventricles are pumping blood into the arteries

trachea

the cartilaginous tube that transports air from the throat to the lungs

tricuspid valve

a one-way opening between the atrium and the ventricle in the right side of the heart

vein

a blood vessel that brings blood back to the heart

ventricle

(of the heart) a large chamber of the heart that pumps blood into arteries

Endocrine System

By the end of this section, you will be able to:

- List the different types of hormones and explain their roles in maintaining homeostasis
- Explain how hormones work
- Explain how hormone production is regulated
- Describe the role of different glands in the endocrine system
- Explain how the different glands work together to maintain homeostasis

The endocrine system produces hormones that function to control and regulate many different body processes. The endocrine system coordinates with the nervous system to control the functions of the other organ systems. Cells of the endocrine system produce molecular signals called hormones. These cells may compose endocrine glands, may be tissues or may be located in organs or tissues that have functions in addition to hormone production. Hormones circulate throughout the body and stimulate a response in cells that have receptors able to bind with them. The changes brought about in the receiving cells affect the functioning of the organ system to which they belong. Many of the hormones are secreted in response to signals from the nervous system, thus the two systems act in concert to effect changes in the body.

Hormones

Maintaining homeostasis within the body requires the coordination of many different systems and organs. One mechanism of communication between neighboring cells, and between cells and tissues in distant parts of the body, occurs through the release of chemicals called hormones. **Hormones** are released into body fluids, usually blood, which carries them to their target cells where they elicit a response. The cells that secrete hormones are often located in specific organs, called **endocrine glands**, and the cells, tissues, and organs that secrete hormones make up the endocrine system. Examples of endocrine organs include the pancreas, which produces the hormones insulin and glucagon to regulate blood-glucose levels, the adrenal glands, which produce hormones such as epinephrine and norepinephrine that

regulate responses to stress, and the thyroid gland, which produces thyroid hormones that regulate metabolic rates.

The endocrine glands differ from the exocrine glands. **Exocrine glands** secrete chemicals through ducts that lead outside the gland (not to the blood). For example, sweat produced by sweat glands is released into ducts that carry sweat to the surface of the skin. The pancreas has both endocrine and exocrine functions because besides releasing hormones into the blood. It also produces digestive juices, which are carried by ducts into the small intestine.

Note:

Career in Action

Endocrinologist

An endocrinologist is a medical doctor who specializes in treating endocrine disorders. An endocrine surgeon specializes in the surgical treatment of endocrine diseases and glands. Some of the diseases that are managed by endocrinologists include disorders of the pancreas (diabetes mellitus), disorders of the pituitary (gigantism, acromegaly, and pituitary dwarfism), disorders of the thyroid gland (goiter and Graves' disease), and disorders of the adrenal glands (Cushing's disease and Addison's disease). Endocrinologists are required to assess patients and diagnose endocrine disorders through extensive use of laboratory tests. Many endocrine diseases are diagnosed using tests that stimulate or suppress endocrine organ functioning. Blood samples are then drawn to determine the effect of stimulating or suppressing an endocrine organ on the production of hormones. For example, to diagnose diabetes mellitus, patients are required to fast for 12 to 24 hours. They are then given a sugary drink, which stimulates the pancreas to produce insulin to decrease blood-glucose levels. A blood sample is taken one to two hours after the sugar drink is consumed. If the pancreas is functioning properly, the blood-glucose level will be within a normal range. Another example is the A1C test, which can be performed during blood screening. The A1C test measures average blood-glucose levels over the past two to three months. The A1C test is an indicator of how well blood glucose is being managed over a long time.

Once a disease such as diabetes has been diagnosed, endocrinologists can prescribe lifestyle changes and medications to treat the disease. Some cases of diabetes mellitus can be managed by exercise, weight loss, and a healthy diet; in other cases, medications may be required to enhance insulin's production or effect. If the disease cannot be controlled by these means, the endocrinologist may prescribe insulin injections.

In addition to clinical practice, endocrinologists may also be involved in primary research and development activities. For example, ongoing islet transplant research is investigating how healthy pancreas islet cells may be transplanted into diabetic patients. Successful islet transplants may allow patients to stop taking insulin injections.

How Hormones Work

Hormones cause changes in target cells by binding to specific cell-surface or **intracellular hormone receptors**, molecules embedded in the cell membrane or floating in the cytoplasm with a binding site that matches a binding site on the hormone molecule. In this way, even though hormones circulate throughout the body and come into contact with many different cell types, they only affect cells that possess the necessary receptors.

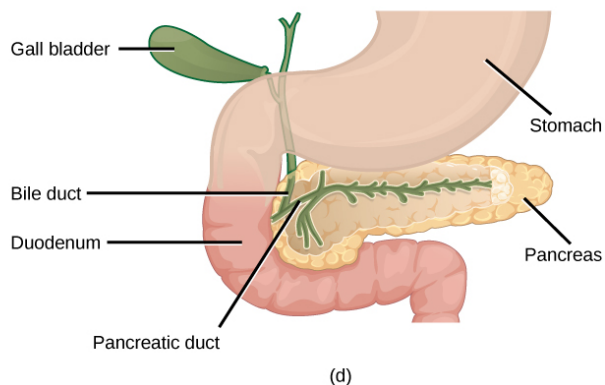
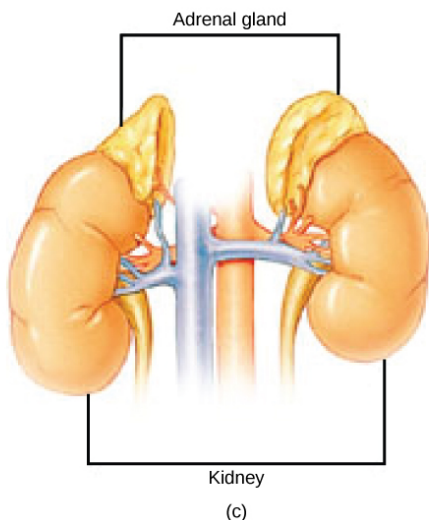
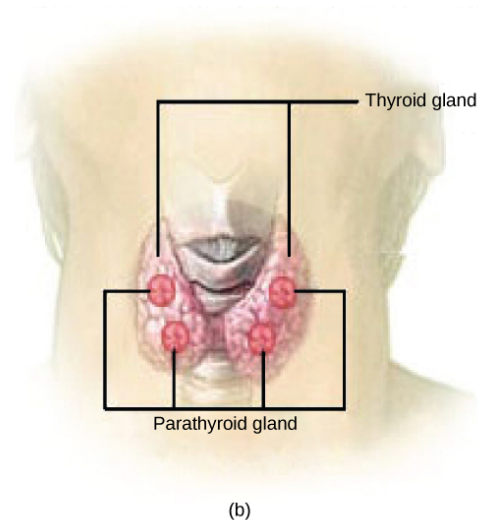
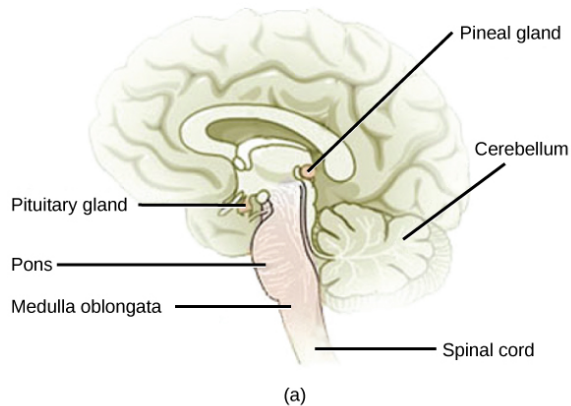
Receptors for a specific hormone may be found on or in many different cells or may be limited to a small number of specialized cells. For example, thyroid hormones act on many different tissue types, stimulating metabolic activity throughout the body. Cells can have many receptors for the same hormone but often also possess receptors for different types of hormones. The number of receptors that respond to a hormone determines the cell's sensitivity to that hormone, and the resulting cellular response.

Additionally, the number of receptors available to respond to a hormone can change over time, resulting in increased or decreased cell sensitivity. In **up-regulation**, the number of receptors increases in response to rising hormone levels, making the cell more sensitive to the hormone and allowing for more cellular activity. When the number of receptors decreases in response to rising hormone levels, called **down-regulation**, cellular activity is reduced.

Endocrine Glands

The endocrine glands secrete hormones into the surrounding interstitial fluid; those hormones then diffuse into blood and are carried to various organs and tissues within the body. The endocrine glands include the pituitary, thyroid, parathyroid, adrenal glands, gonads, pineal, and pancreas.

The **pituitary gland**, sometimes called the hypophysis, is located at the base of the brain ([link](#)a). It is attached to the hypothalamus. The posterior lobe stores and releases oxytocin and antidiuretic hormone produced by the hypothalamus. The anterior lobe responds to hormones produced by the hypothalamus by producing its own hormones, most of which regulate other hormone-producing glands.



(a) The pituitary gland sits at the base of the brain, just above the brain stem. (b) The parathyroid glands are located on the posterior of the thyroid gland. (c) The adrenal glands are on top of the kidneys. d) The pancreas is found between the stomach and the small intestine. (credit: modification of work by NCI, NIH)

The anterior pituitary produces six hormones: growth hormone, prolactin, thyroid-stimulating hormone, adrenocorticotropic hormone, follicle-stimulating hormone, and luteinizing hormone. Growth hormone stimulates cellular activities like protein synthesis that promote growth. Prolactin stimulates the production of milk by the mammary glands. The other hormones produced by the anterior pituitary regulate the production of hormones by other endocrine tissues ([\[link\]](#)). The posterior pituitary is significantly different in structure from the anterior pituitary. It is a part of the brain, extending down from the hypothalamus, and contains mostly nerve fibers that extend from the hypothalamus to the posterior pituitary.

The **thyroid gland** is located in the neck, just below the larynx and in front of the trachea ([\[link\]](#)**b**). It is a butterfly-shaped gland with two lobes that are connected. The thyroid follicle cells synthesize the hormone thyroxine, which is also known as T_4 because it contains four atoms of iodine, and triiodothyronine, also known as T_3 because it contains three atoms of iodine. T_3 and T_4 are released by the thyroid in response to thyroid-stimulating hormone produced by the anterior pituitary, and both T_3 and T_4 have the effect of stimulating metabolic activity in the body and increasing energy use. A third hormone, calcitonin, is also produced by the thyroid. Calcitonin is released in response to rising calcium ion concentrations in the blood and has the effect of reducing those levels.

Most people have four **parathyroid glands**; however, the number can vary from two to six. These glands are located on the posterior surface of the thyroid gland ([\[link\]](#)**b**).

The parathyroid glands produce parathyroid hormone. Parathyroid hormone increases blood calcium concentrations when calcium ion levels fall below normal.

The **adrenal glands** are located on top of each kidney ([link](#)c). The adrenal glands consist of an outer adrenal cortex and an inner adrenal medulla. These regions secrete different hormones.

The adrenal cortex produces mineralocorticoids, glucocorticoids, and androgens. The main mineralocorticoid is aldosterone, which regulates the concentration of ions in urine, sweat, and saliva. Aldosterone release from the adrenal cortex is stimulated by a decrease in blood concentrations of sodium ions, blood volume, or blood pressure, or by an increase in blood potassium levels. The glucocorticoids maintain proper blood-glucose levels between meals. They also control a response to stress by increasing glucose synthesis from fats and proteins and interact with epinephrine to cause vasoconstriction. Androgens are sex hormones that are produced in small amounts by the adrenal cortex. They do not normally affect sexual characteristics and may supplement sex hormones released from the gonads. The adrenal medulla contains two types of secretory cells: one that produces epinephrine (adrenaline) and another that produces norepinephrine (noradrenaline). Epinephrine and norepinephrine cause immediate, short-term changes in response to stressors, inducing the so-called fight-or-flight response. The responses include increased heart rate, breathing rate, cardiac muscle contractions, and blood-glucose levels. They also accelerate the breakdown of glucose in skeletal muscles and stored fats in adipose tissue, and redirect blood flow toward skeletal muscles and away from skin and viscera. The release of epinephrine and norepinephrine is stimulated by neural impulses from the sympathetic nervous system that originate from the hypothalamus.

The **pancreas** is an elongate organ located between the stomach and the proximal portion of the small intestine ([link](#)d). It contains both exocrine cells that excrete digestive enzymes and endocrine cells that release hormones.

The endocrine cells of the pancreas form clusters called pancreatic islets or the islets of Langerhans. Among the cell types in each pancreatic islet are

the alpha cells, which produce the hormone glucagon, and the beta cells, which produce the hormone insulin. These hormones regulate blood-glucose levels. Alpha cells release glucagon as blood-glucose levels decline. When blood-glucose levels rise, beta cells release insulin. Glucagon causes the release of glucose to the blood from the liver, and insulin facilitates the uptake of glucose by the body's cells.

The gonads—the male testes and female ovaries—produce steroid hormones. The testes produce androgens, testosterone being the most prominent, which allow for the development of secondary sex characteristics and the production of sperm cells. The ovaries produce estrogen and progesterone, which cause secondary sex characteristics, regulate production of eggs, control pregnancy, and prepare the body for childbirth.

There are several organs whose primary functions are non-endocrine but that also possess endocrine functions. These include the heart, kidneys, intestines, thymus, and adipose tissue. The heart has endocrine cells in the walls of the atria that release a hormone in response to increased blood volume. It causes a reduction in blood volume and blood pressure, and reduces the concentration of Na^+ in the blood.

The gastrointestinal tract produces several hormones that aid in digestion. The endocrine cells are located in the mucosa of the GI tract throughout the stomach and small intestine. They trigger the release of gastric juices, which help to break down and digest food in the GI tract.

The kidneys also possess endocrine function. Two of these hormones regulate ion concentrations and blood volume or pressure. Erythropoietin (EPO) is released by kidneys in response to low oxygen levels. EPO triggers the formation of red blood cells in the bone marrow. EPO has been used by athletes to improve performance. But EPO doping has its risks, since it thickens the blood and increases strain on the heart; it also increases the risk of blood clots and therefore heart attacks and stroke.

The **thymus** is found behind the sternum. The thymus produces hormones referred to as thymosins, which contribute to the development of the immune response in infants. Adipose tissue, or fat tissue, produces the

hormone leptin in response to food intake. Leptin produces a feeling of satiety after eating, reducing the urge for further eating.

Endocrine Glands and Their Associated Hormones		
Endocrine Gland	Associated Hormones	Effect
Pituitary (anterior)	growth hormone	promotes growth of body tissues
	prolactin	promotes milk production
	thyroid-stimulating hormone	stimulates thyroid hormone release
	adrenocorticotropic hormone	stimulates hormone release by adrenal cortex
	follicle-stimulating hormone	stimulates gamete production
	luteinizing hormone	stimulates androgen production by gonads in males; stimulates ovulation and production of estrogen and progesterone in females
Pituitary (posterior)	antidiuretic hormone	stimulates water reabsorption by kidneys

Endocrine Glands and Their Associated Hormones		
Endocrine Gland	Associated Hormones	Effect
	oxytocin	stimulates uterine contractions during childbirth
Thyroid	thyroxine, triiodothyronine	stimulate metabolism
	calcitonin	reduces blood Ca^{2+} levels
Parathyroid	parathyroid hormone	increases blood Ca^{2+} levels
Adrenal (cortex)	aldosterone	increases blood Na^{+} levels
	cortisol, corticosterone, cortisone	increase blood-glucose levels
Adrenal (medulla)	epinephrine, norepinephrine	stimulate fight-or-flight response
Pancreas	insulin	reduces blood-glucose levels
	glucagon	increases blood-glucose levels

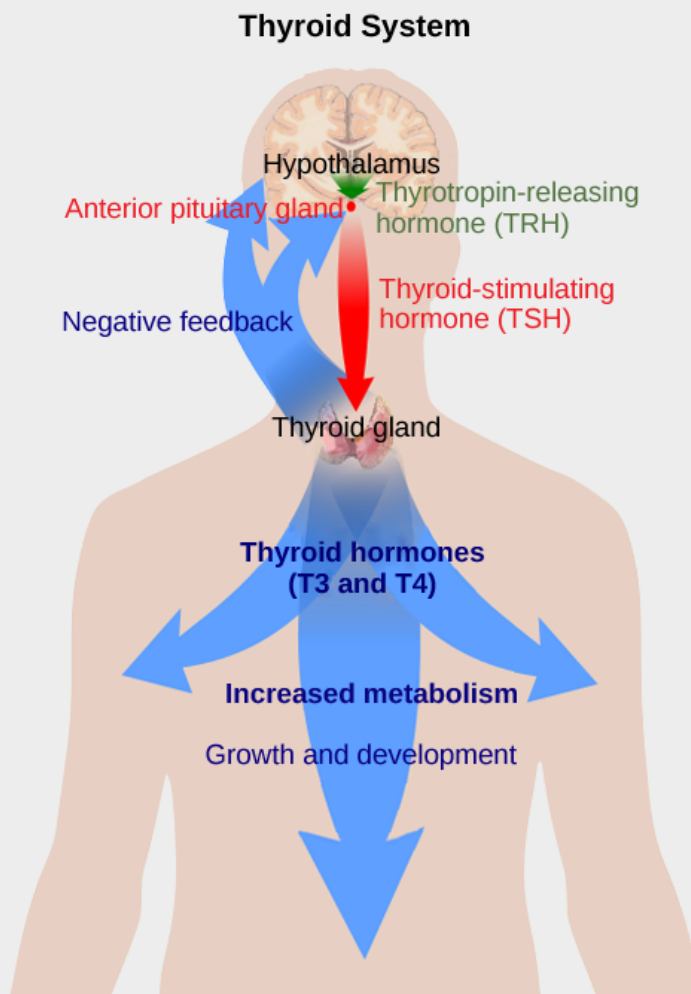
Regulation of Hormone Production

Hormone production and release are primarily controlled by negative feedback, as described in the discussion on homeostasis. In this way, the

concentration of hormones in blood is maintained within a narrow range. For example, the anterior pituitary signals the thyroid to release thyroid hormones. Increasing levels of these hormones in the blood then give feedback to the hypothalamus and anterior pituitary to inhibit further signaling to the thyroid gland ([link](#)).

Note:

Art Connection



The anterior pituitary stimulates the thyroid gland to release thyroid hormones T_3 and T_4 . Increasing levels of these hormones in the blood result in feedback to the hypothalamus and anterior

pituitary to inhibit further signaling to the thyroid gland. (credit: modification of work by Mikael Häggström)

Goiter, a disease caused by iodine deficiency, results in the inability of the thyroid gland to form T_3 and T_4 . The body typically attempts to compensate by producing greater amounts of TSH. Which of the following symptoms would you expect goiter to cause?

- a. Hypothyroidism, resulting in weight gain, cold sensitivity, and reduced mental activity.
- b. Hyperthyroidism, resulting in weight loss, profuse sweating, and increased heart rate.
- c. Hyperthyroidism, resulting in weight gain, cold sensitivity, and reduced mental activity.
- d. Hypothyroidism, resulting in weight loss, profuse sweating, and increased heart rate.

Section Summary

Hormones cause cellular changes by binding to receptors on or in target cells. The number of receptors on a target cell can increase or decrease in response to hormone activity.

Hormone levels are primarily controlled through negative feedback, in which rising levels of a hormone inhibit its further release.

The pituitary gland is located at the base of the brain. The anterior pituitary receives signals from the hypothalamus and produces six hormones. The posterior pituitary is an extension of the brain and releases hormones (antidiuretic hormone and oxytocin) produced by the hypothalamus. The thyroid gland is located in the neck and is composed of two lobes. The thyroid produces the hormones thyroxine and triiodothyronine. The thyroid

also produces calcitonin. The parathyroid glands lie on the posterior surface of the thyroid gland and produce parathyroid hormone.

The adrenal glands are located on top of the kidneys and consist of the adrenal cortex and adrenal medulla. The adrenal cortex produces the corticosteroids, glucocorticoids and mineralocorticoids. The adrenal medulla is the inner part of the adrenal gland and produces epinephrine and norepinephrine.

The pancreas lies in the abdomen between the stomach and the small intestine. Clusters of endocrine cells in the pancreas form the islets of Langerhans, which contain alpha cells that release glucagon and beta cells that release insulin. Some organs possess endocrine activity as a secondary function but have another primary function. The heart produces the hormone atrial natriuretic peptide, which functions to reduce blood volume, pressure, and Na^+ concentration. The gastrointestinal tract produces various hormones that aid in digestion. The kidneys produce erythropoietin. The thymus produces hormones that aid in the development of the immune system. The gonads produce steroid hormones, including testosterone in males and estrogen and progesterone in females. Adipose tissue produces leptin, which promotes satiety signals in the brain.

Art Connections

Exercise:

Problem:

[\[link\]](#) Goiter, a disease caused by iodine deficiency, results in the inability of the thyroid gland to form T_3 and T_4 . The body typically attempts to compensate by producing greater amounts of TSH. Which of the following symptoms would you expect goiter to cause?

- a. Hypothyroidism, resulting in weight gain, cold sensitivity, and reduced mental activity.
- b. Hyperthyroidism, resulting in weight loss, profuse sweating and increased heart rate.

- c. Hyperthyroidism, resulting in weight gain, cold sensitivity, and reduced mental activity.
 - d. Hypothyroidism, resulting in weight loss, profuse sweating and increased heart rate.
-

Solution:

[\[link\]](#) A

Review Questions

Exercise:

Problem:

Most of the hormones produced by the anterior pituitary perform what function?

- a. regulate growth
 - b. regulate the sleep cycle
 - c. regulate production of other hormones
 - d. regulate blood volume and blood pressure
-

Solution:

C

Exercise:

Problem:What is the function of the hormone erythropoietin?

- a. stimulates production of red blood cells
 - b. stimulates muscle growth
 - c. causes the fight-or-flight response
 - d. causes testosterone production
-

Solution:

A

Exercise:

Problem: Which endocrine glands are associated with the kidneys?

- a. thyroid glands
- b. pituitary glands
- c. adrenal glands
- d. gonads

Solution:

C

Free Response

Exercise:

Problem:

What is a similarity and a difference between an exocrine gland and an endocrine gland?

Solution:

The cells of both exocrine and endocrine glands produce a product that will be secreted by the gland. An exocrine gland has a duct and secretes its product to the outside of the gland, not into the bloodstream. An endocrine gland secretes its product into the bloodstream and does not use a duct.

Exercise:

Problem:

Describe how hormone receptors can play a role in affecting the size of the responses of tissues to hormones.

Solution:

The number of receptors that respond to a hormone can change, resulting in increased or decreased cell sensitivity. The number of receptors can increase in response to rising hormone levels, called up-regulation, making the cell more sensitive to the hormone and allowing for more cellular activity. The number of receptors can also decrease in response to rising hormone levels, called down-regulation, leading to reduced cellular activity.

Exercise:**Problem:**

Many hormone systems regulate body functions through opposing hormone actions. Describe how opposing hormone actions regulate blood-glucose levels?

Solution:

Blood-glucose levels are regulated by hormones produced by the pancreas: insulin and glucagon. When blood-glucose levels are increasing, the pancreas releases insulin, which stimulates uptake of glucose by cells. When blood-glucose levels are decreasing, the pancreas releases glucagon, which stimulates the release of stored glucose by the liver to the bloodstream.

Glossary

adrenal gland

the endocrine gland associated with the kidneys

down-regulation

a decrease in the number of hormone receptors in response to increased hormone levels

endocrine gland

the gland that secretes hormones into the surrounding interstitial fluid, which then diffuse into blood and are carried to various organs and tissues within the body

exocrine gland

the gland that secretes chemicals through ducts that lead to skin surfaces, body cavities, and organ cavities.

hormone

a chemical released by cells in one area of the body that affects cells in other parts of the body

intracellular hormone receptor

a hormone receptor in the cytoplasm or nucleus of a cell

pancreas

the organ located between the stomach and the small intestine that contains exocrine and endocrine cells

parathyroid gland

the gland located on the surface of the thyroid that produces parathyroid hormone

pituitary gland

the endocrine gland located at the base of the brain composed of an anterior and posterior region; also called hypophysis

thymus

the gland located behind the sternum that produces thymosin hormones that contribute to the development of the immune system

thyroid gland

an endocrine gland located in the neck that produces thyroid hormones thyroxine and triiodothyronine

up-regulation

an increase in the number of hormone receptors in response to increased hormone levels

Musculoskeletal System

By the end of this section, you will be able to:

- Discuss the axial and appendicular parts of the skeletal system
- Explain the role of joints in skeletal movement
- Explain the role of muscles in locomotion

The muscular and skeletal systems provide support to the body and allow for movement. The bones of the skeleton protect the body's internal organs and support the weight of the body. The muscles of the muscular system contract and pull on the bones, allowing for movements as diverse as standing, walking, running, and grasping items.

Injury or disease affecting the musculoskeletal system can be very debilitating. The most common musculoskeletal diseases worldwide are caused by malnutrition, which can negatively affect development and maintenance of bones and muscles. Other diseases affect the joints, such as arthritis, which can make movement difficult and, in advanced cases, completely impair mobility.

Progress in the science of prosthesis design has resulted in the development of artificial joints, with joint replacement surgery in the hips and knees being the most common. Replacement joints for shoulders, elbows, and fingers are also available.

Skeletal System

The human skeleton is an endoskeleton that consists of 206 bones in the adult. An endoskeleton develops within the body rather than outside like the exoskeleton of insects. The skeleton has five main functions: providing support to the body, storing minerals and lipids, producing blood cells, protecting internal organs, and allowing for movement. The skeletal system in vertebrates is divided into the axial skeleton (which consists of the skull, vertebral column, and rib cage), and the appendicular skeleton (which consists of limb bones, the pectoral or shoulder girdle, and the pelvic girdle).

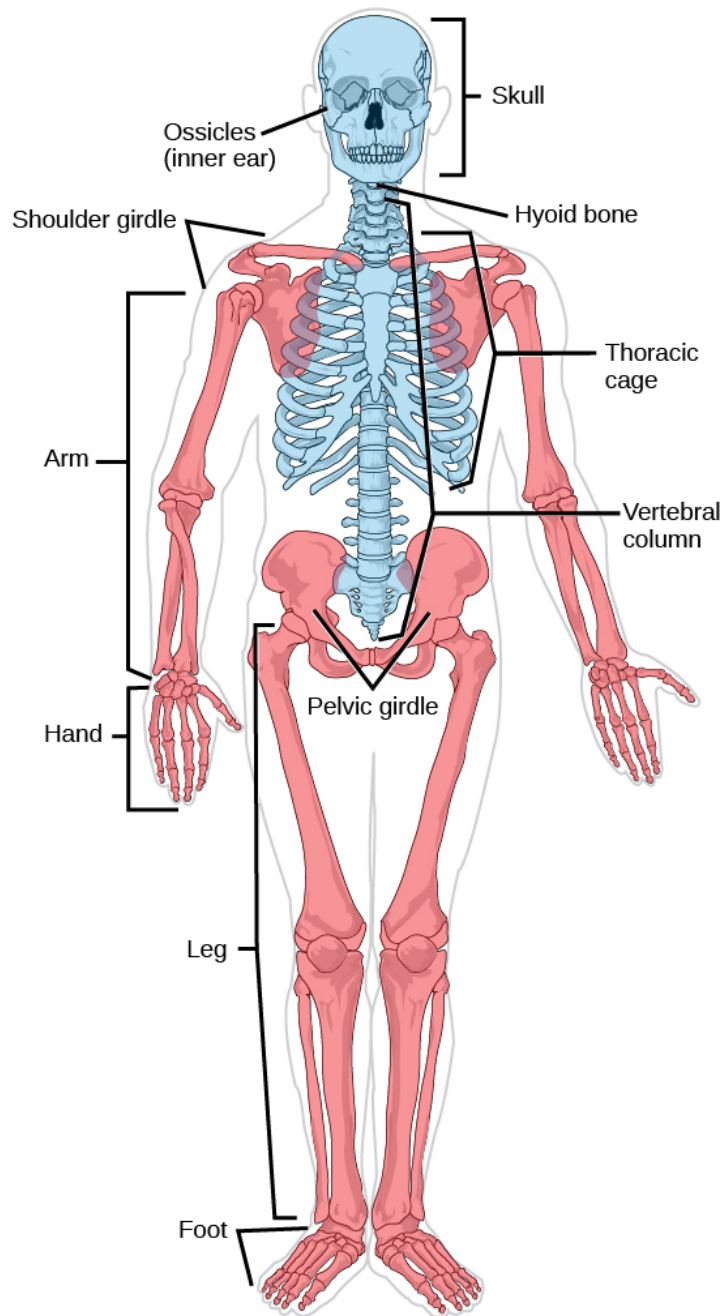
Note:

Concept in Action



Explore the human skeleton by viewing the following [video](#) with digital 3D sculpturing.

The **axial skeleton** forms the central axis of the body and includes the bones of the skull, ossicles of the middle ear, hyoid bone of the throat, vertebral column, and the thoracic cage (rib cage) ([link](#)).



The axial skeleton, shown in blue, consists of the bones of the skull, ossicles of the middle ear, hyoid bone, vertebral column, and thoracic cage. The appendicular skeleton, shown in red, consists of the bones of the pectoral limbs, pectoral girdle, pelvic

limb, and pelvic girdle. (credit:
modification of work by Mariana Ruiz
Villareal)

The bones of the **skull** support the structures of the face and protect the brain. The skull consists of cranial bones and facial bones. The cranial bones form the cranial cavity, which encloses the brain and serves as an attachment site for muscles of the head and neck. In the adult they are tightly jointed with connective tissue and adjoining bones do not move.

The **auditory ossicles** of the middle ear transmit sounds from the air as vibrations to the fluid-filled cochlea. The auditory ossicles consist of two malleus (hammer) bones, two incus (anvil) bones, and two stapes (stirrups), one on each side. Facial bones provide cavities for the sense organs (eyes, mouth, and nose), and serve as attachment points for facial muscles.

The **hyoid bone** lies below the mandible in the front of the neck. It acts as a movable base for the tongue and is connected to muscles of the jaw, larynx, and tongue. The mandible forms a joint with the base of the skull. The mandible controls the opening to the mouth and hence, the airway and gut.

The **vertebral column**, or spinal column, surrounds and protects the spinal cord, supports the head, and acts as an attachment point for ribs and muscles of the back and neck. It consists of 26 bones: the 24 vertebrae, the sacrum, and the coccyx. Each vertebral body has a large hole in the center through which the spinal cord passes down to the level of the first lumbar vertebra. Below this level, the hole contains spinal nerves which exit between the vertebrae. There is a notch on each side of the hole through which the spinal nerves, can exit from the spinal cord to serve different regions of the body. The vertebral column is approximately 70 cm (28 in) in adults and is curved, which can be seen from a side view.

Intervertebral discs composed of fibrous cartilage lie between adjacent vertebrae from the second cervical vertebra to the sacrum. Each disc helps form a slightly moveable joint and acts as a cushion to absorb shocks from movements such as walking and running.

The **thoracic cage**, also known as the rib cage consists of the ribs, sternum, thoracic vertebrae, and costal cartilages. The thoracic cage encloses and protects the organs of the thoracic cavity including the heart and lungs. It also provides support for the shoulder girdles and upper limbs and serves as the attachment point for the diaphragm, muscles of the back, chest, neck, and shoulders. Changes in the volume of the thorax enable breathing. The sternum, or breastbone, is a long flat bone located at the anterior of the chest. Like the skull, it is formed from many bones in the embryo, which fuse in the adult. The ribs are 12 pairs of long curved bones that attach to the thoracic vertebrae and curve toward the front of the body, forming the ribcage. Costal cartilages connect the anterior ends of most ribs to the sternum.

The **appendicular skeleton** is composed of the bones of the upper and lower limbs. It also includes the pectoral, or shoulder girdle, which attaches the upper limbs to the body, and the pelvic girdle, which attaches the lower limbs to the body ([link](#)).

The **pectoral girdle** bones transfer force generated by muscles acting on the upper limb to the thorax. It consists of the clavicles (or collarbones) in the anterior, and the scapulae (or shoulder blades) in the posterior.

The upper limb contains bones of the arm (shoulder to elbow), the forearm, and the hand. The humerus is the largest and longest bone of the upper limb. It forms a joint with the shoulder and with the forearm at the elbow. The forearm extends from the elbow to the wrist and consists of two bones. The hand includes the bones of the wrist, the palm, and the bones of the fingers.

The **pelvic girdle** attaches to the lower limbs of the axial skeleton. Since it is responsible for bearing the weight of the body and for locomotion, the pelvic girdle is securely attached to the axial skeleton by strong ligaments. It also has deep sockets with robust ligaments that securely attach to the femur. The pelvic girdle is mainly composed of two large hip bones. The hip bones join together in the anterior of the body at a joint called the pubic symphysis and with the bones of the sacrum at the posterior of the body.

The lower limb consists of the thigh, the leg, and the foot. The bones of the lower limbs are thicker and stronger than the bones of the upper limbs to support the entire weight of the body and the forces from locomotion. The femur, or thighbone, is the longest, heaviest, and strongest bone in the body. The femur and pelvis form the hip joint. At its other end, the femur, along with the shinbone and kneecap, form the knee joint.

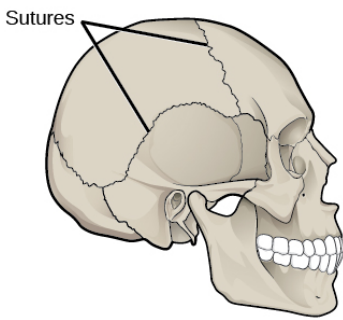
Joints and Skeletal Movement

The point at which two or more bones meet is called a **joint**, or articulation. Joints are responsible for movement, such as the movement of limbs, and stability, such as the stability found in the bones of the skull.

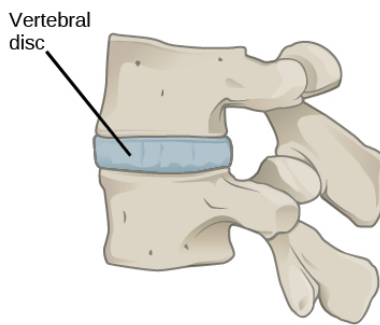
There are two ways to classify joints: based on their structure or based on their function. The structural classification divides joints into fibrous, cartilaginous, and synovial joints depending on the material composing the joint and the presence or absence of a cavity in the joint. The bones of **fibrous joints** are held together by fibrous connective tissue. There is no cavity, or space, present between the bones, so most fibrous joints do not move at all, or are only capable of minor movements. The joints between the bones in the skull and between the teeth and the bone of their sockets are examples of fibrous joints ([\[link\]](#)**a**).

Cartilaginous joints are joints in which the bones are connected by cartilage ([\[link\]](#)**b**). An example is found at the joints between vertebrae, the so-called “disks” of the backbone. Cartilaginous joints allow for very little movement.

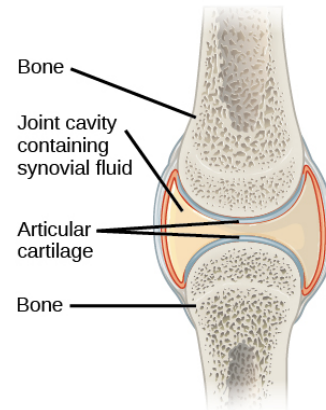
Synovial joints are the only joints that have a space between the adjoining bones ([\[link\]](#)**c**). This space is referred to as the joint cavity and is filled with fluid. The fluid lubricates the joint, reducing friction between the bones and allowing for greater movement. The ends of the bones are covered with cartilage and the entire joint is surrounded by a capsule. Synovial joints are capable of the greatest movement of the joint types. Knees, elbows, and shoulders are examples of synovial joints.



(a)



(b)



(c)

- (a) Sutures are fibrous joints found only in the skull. (b) Cartilaginous joints are bones connected by cartilage, such as between vertebrae. (c) Synovial joints are the only joints that have a space or “synovial cavity” in the joint.

The wide range of movement allowed by synovial joints produces different types of movements. Angular movements are produced when the angle between the bones of a joint changes. Flexion, or bending, occurs when the angle between the bones decreases. Moving the forearm upward at the elbow is an example of flexion. Extension is the opposite of flexion in that the angle between the bones of a joint increases. Rotational movement is the movement of a bone as it rotates around its own longitudinal axis. Movement of the head as in saying “no” is an example of rotation.

Note:

Career in Action

Rheumatologist

Rheumatologists are medical doctors who specialize in the diagnosis and treatment of disorders of the joints, muscles, and bones. They diagnose and treat diseases such as arthritis, musculoskeletal disorders, osteoporosis, plus autoimmune diseases like ankylosing spondylitis, a chronic spinal inflammatory disease and rheumatoid arthritis.

Rheumatoid arthritis (RA) is an inflammatory disorder that primarily affects synovial joints of the hands, feet, and cervical spine. Affected joints become swollen, stiff, and painful. Although it is known that RA is an autoimmune disease in which the body's immune system mistakenly attacks healthy tissue, the exact cause of RA remains unknown. Immune cells from the blood enter joints and the joint capsule causing cartilage breakdown and swelling of the joint lining. Breakdown of cartilage causes bones to rub against each other causing pain. RA is more common in women than men and the age of onset is usually between 40 to 50 years. Rheumatologists can diagnose RA based on symptoms such as joint inflammation and pain, x-ray and MRI imaging, and blood tests.

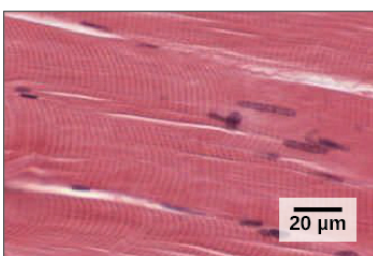
Arthrography is a type of medical imaging of joints that uses a contrast agent, such as a dye that is opaque to x-rays. This allows the soft tissue structures of joints—such as cartilage, tendons, and ligaments—to be visualized. An arthrogram differs from a regular x-ray by showing the surface of soft tissues lining the joint in addition to joint bones. An arthrogram allows early degenerative changes in joint cartilage to be detected before bones become affected.

There is currently no cure for RA; however, rheumatologists have a number of treatment options available. Treatments are divided into those that reduce the symptoms of the disease and those that reduce the damage to bone and cartilage caused by the disease. Early stages can be treated with rest of the affected joints through the use of a cane, or with joint splints that minimize inflammation. When inflammation has decreased, exercise can be used to strengthen muscles that surround the joint and to maintain joint flexibility. If joint damage is more extensive, medications can be used to relieve pain and decrease inflammation. Anti-inflammatory drugs that may be used include aspirin, topical pain relievers, and corticosteroid injections. Surgery may be required in cases where joint damage is severe. Physicians are now using drugs that reduce the damage to bones and cartilage caused by the disease to slow its development.

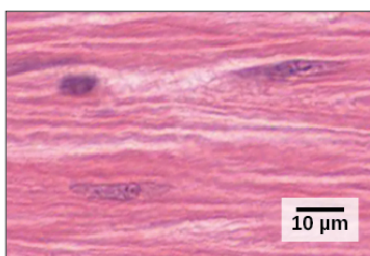
These drugs are diverse in their mechanisms but they all act to reduce the impact of the autoimmune response, for example by inhibiting the inflammatory response or reducing the number of T lymphocytes, a cell of the immune system.

Muscles

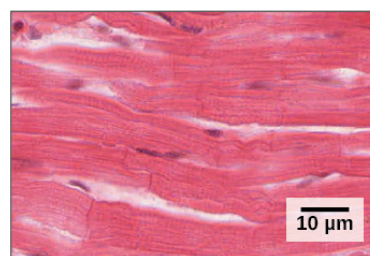
Muscles allow for movement such as walking, and they also facilitate bodily processes such as respiration and digestion. The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle ([link](#)).



Skeletal muscle



Smooth muscle



Cardiac muscle

The body contains three types of muscle tissue: skeletal muscle, smooth muscle, and cardiac muscle. Notice that skeletal muscle cells are long and cylindrical, they have multiple nuclei, and the small, dark nuclei are pushed to the periphery of the cell. Smooth muscle cells are short, tapered at each end, and have only one nucleus each. Cardiac muscle cells are also cylindrical, but short. The cytoplasm may branch, and they have one or two nuclei in the center of the cell. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)

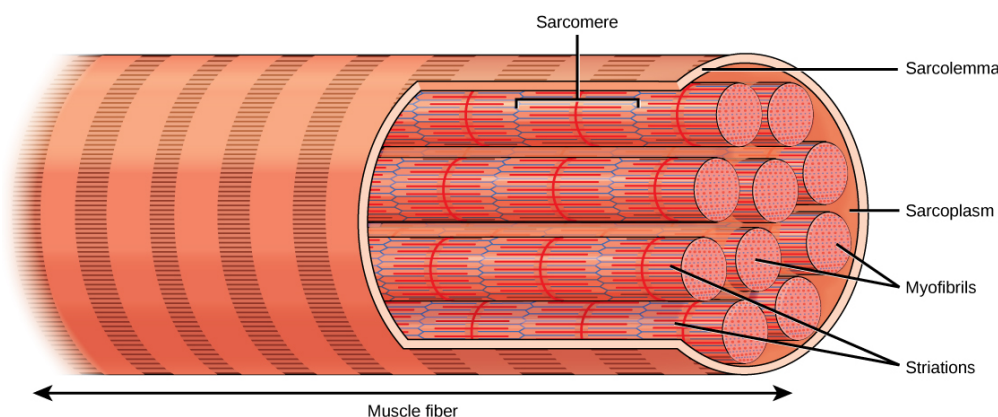
Skeletal muscle tissue forms skeletal muscles, which attach to bones and sometimes the skin and control locomotion and any other movement that can be consciously controlled. Because it can be controlled intentionally, skeletal muscle is also called voluntary muscle. When viewed under a microscope, skeletal muscle tissue has a striped or striated appearance. This appearance results from the arrangement of the proteins inside the cell that are responsible for contraction. The cells of skeletal muscle are long and tapered and have multiple nuclei on the periphery of each cell.

Smooth muscle tissue occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as in the respiratory tract and blood vessels. Smooth muscle has no striations, is not under voluntary control, and is called involuntary muscle. Smooth muscle cells have a single nucleus.

Cardiac muscle tissue is only found in the heart. The contractions of cardiac muscle tissue pump blood throughout the body and maintain blood pressure. Like skeletal muscle, cardiac muscle is striated, but unlike skeletal muscle, cardiac muscle cannot be consciously controlled and is called involuntary muscle. The cells of cardiac muscle tissue are connected to each other through intercalated disks and usually have just one nucleus per cell.

Skeletal Muscle Fiber Structure and Function

Each skeletal muscle fiber is a skeletal muscle cell. Within each muscle fiber are **myofibrils**, long cylindrical structures that lie parallel to the muscle fiber. Myofibrils run the entire length of the muscle fiber. They attach to the plasma membrane, called the **sarcolemma**, at their ends, so that as myofibrils shorten, the entire muscle cell contracts ([\[link\]](#)).



A skeletal muscle fiber is surrounded by a plasma membrane called the sarcolemma, with a cytoplasm called the sarcoplasm. A muscle fiber is composed of

many fibrils packaged into orderly units. The orderly arrangement of the proteins in each unit, shown as red and blue lines, gives the cell its striated appearance.

The striated appearance of skeletal muscle tissue is a result of repeating bands of the proteins actin and myosin that occur along the length of myofibrils.

Myofibrils are composed of smaller structures called **myofilaments**. There are two main types of myofilaments: thick filaments and thin filaments. Thick filaments are composed of the protein myosin. The primary component of thin filaments is the protein actin.

The thick and thin filaments alternate with each other in a structure called a **sarcomere**. The sarcomere is the unit of contraction in a muscle cell. Contraction is stimulated by an electrochemical signal from a nerve cell associated with the muscle fiber. For a muscle cell to contract, the sarcomere must shorten. However, thick and thin filaments do not shorten. Instead, they slide by one another, causing the sarcomere to shorten while the filaments remain the same length. The sliding is accomplished when a molecular extension of myosin, called the myosin head, temporarily binds to an actin filament next to it and through a change in conformation, bends, dragging the two filaments in opposite directions. The myosin head then releases its actin filament, relaxes, and then repeats the process, dragging the two filaments further along each other. The combined activity of many binding sites and repeated movements within the sarcomere causes it to contract. The coordinated contractions of many sarcomeres in a myofibril leads to contraction of the entire muscle cell and ultimately the muscle itself. The movement of the myosin head requires ATP, which provides the energy for the contraction.

Note:

Concept in Action



View this [animation](#) to see how muscle fibers are organized.

Section Summary

The human skeleton is an endoskeleton that is composed of the axial and appendicular skeleton. The axial skeleton is composed of the bones of the skull, ossicles of the ear, hyoid bone, vertebral column, and ribcage. The skull consists of eight cranial bones and 14 facial bones. Six bones make up the ossicles of the middle ear, while the hyoid bone is located in the neck under the mandible. The vertebral column contains 26 bones and surrounds and protects the spinal cord. The thoracic cage consists of the sternum, ribs, thoracic vertebrae, and costal cartilages. The appendicular skeleton is made up of the upper and lower limbs. The pectoral girdle is composed of the clavicles and the scapulae. The upper limb contains 30 bones in the arm, the forearm, and the hand. The pelvic girdle attaches the lower limbs to the axial skeleton. The lower limb includes the bones of the thigh, the leg, and the foot.

The structural classification of joints divides them into fibrous, cartilaginous, and synovial joints. The bones of fibrous joints are held together by fibrous connective tissue. Cartilaginous joints are joints in which the bones are connected by cartilage. Synovial joints are joints that have a space between the adjoining bones. The movement of synovial joints includes angular and rotational. Angular movements are produced when the angle between the bones of a joint changes. Rotational movement is the movement of a bone as it rotates around its own longitudinal axis.

The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle. Muscles are composed of individual cells

called muscle fibers. Muscle fibers consist of myofilaments composed of the proteins actin and myosin arranged in units called sarcomeres. Contraction of the muscle occurs by the combined action of myosin and actin fibers sliding past each other when the myosin heads bind to the actin fiber, bend, disengage, and then repeat the process.

Review Questions

Exercise:

Problem:

Among other bones, the axial skeleton includes the _____.

- a. thoracic cage and vertebral column
- b. thoracic cage and pectoral girdle
- c. skull and pelvic girdle
- d. pectoral and pelvic girdles

Solution:

A

Exercise:

Problem: The pectoral girdle supports the _____.

- a. arms
- b. legs
- c. skull
- d. thoracic cage

Solution:

A

Exercise:

Problem:

Which component is responsible for initially stimulating a muscle contraction?

- a. proteins
- b. electrochemical signals
- c. plasma membranes
- d. striations

Solution:

B

Exercise:**Problem:**

What kind of muscle tissue is found surrounding the urinary bladder?

- a. cardiac
- b. skeletal
- c. striated
- d. smooth

Solution:

D

Free Response**Exercise:****Problem:**

What movements occur at the hip joint and knees as you bend down to pick something up?

Solution:

The hip joint is flexed and the knees are extended.

Glossary**appendicular skeleton**

the skeleton composed of the bones of the upper limbs, which function to grasp and manipulate objects, and the lower limbs, which permit locomotion

auditory ossicles

(also, middle ear bones) the bones that transduce sounds from the air into vibrations in the fluid-filled cochlea

axial skeleton

skeleton that forms the central axis of the body and includes the bones of the skull, the ossicles of the middle ear, the hyoid bone of the throat, the vertebral column, and the thoracic cage (ribcage)

cardiac muscle tissue

the muscle tissue found only in the heart; cardiac contractions pump blood throughout the body and maintain blood pressure

cartilaginous joint

a joint in which the bones are connected by cartilage

fibrous joint

a joint held together by fibrous connective tissue

hyoid bone

the bone that lies below the mandible in the front of the neck

joint

the point at which two or more bones meet

myofibril

the long cylindrical structures that lie parallel to the muscle fiber

myofilament

the small structures that make up myofibrils

pectoral girdle

the bones that transmit the force generated by the upper limbs to the axial skeleton

pelvic girdle

the bones that transmit the force generated by the lower limbs to the axial skeleton

sarcolemma

the plasma membrane of a skeletal muscle fiber

sarcomere

the functional unit of skeletal muscle

skeletal muscle tissue

forms skeletal muscles, which attach to bones and control locomotion and any movement that can be consciously controlled

skull

the bone that supports the structures of the face and protects the brain

smooth muscle tissue

the muscle that occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as the respiratory tract and blood vessels

synovial joints

the only joints that have a space between the adjoining bones

thoracic cage

(also, ribcage) the skeleton of the chest, which consists of the ribs, thoracic vertebrae, sternum, and costal cartilages

vertebral column

(also, spine) the column that surrounds and protects the spinal cord, supports the head, and acts as an attachment point for ribs and muscles of the back and neck

Nervous System

By the end of this section, you will be able to:

- Describe the form and function of a neuron
- Describe the basic parts and functions of the central nervous system
- Describe the basic parts and functions of the peripheral nervous system

As you read this, your nervous system is performing several functions simultaneously. The visual system is processing what is seen on the page; the motor system controls your eye movements and the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. The nervous system is one of two systems that exert control over all the organ systems of the body; the other is the endocrine system. The nervous system's control is much more specific and rapid than the hormonal system. It communicates signals through cells and the tiny gaps between them rather than through the circulatory system as in the endocrine system. It uses a combination of chemical and electrochemical signals, rather than purely chemical signals used by the endocrine system to cover long distances quickly. The nervous system acquires information from sensory organs, processes it and then may initiate a response either through motor function, leading to movement, or in a change in the organism's physiological state.

Nervous systems throughout the animal kingdom vary in structure and complexity. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a "nerve net." Flatworms have both a central nervous system (CNS), made up of a ganglion (clusters of connected neurons) and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia. These ganglia can control movements and behaviors without input from the brain.

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that

contains a brain and spinal cord and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally (toward the stomach) whereas the vertebrate spinal cords are located dorsally (toward the back). There is debate among evolutionary biologists as to whether these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow “flipped” during the evolution of vertebrates.

The nervous system is made up of **neurons**, specialized cells that can receive and transmit chemical or electrical signals, and **glia**, cells that provide support functions for the neurons. There is great diversity in the types of neurons and glia that are present in different parts of the nervous system.

Neurons and Glial Cells

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components. Neurons also contain unique structures for receiving and sending the electrical signals that make communication between neurons possible ([\[link\]](#)). **Dendrites** are tree-like structures that extend away from the cell body to receive messages from

other neurons at specialized junctions called **synapses**. Although some neurons do not have any dendrites, most have one or many dendrites.

The bilayer lipid membrane that surrounds a neuron is impermeable to ions. To enter or exit the neuron, ions must pass through ion channels that span the membrane. Some ion channels need to be activated to open and allow ions to pass into or out of the cell. These ion channels are sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. The difference in total charge between the inside and outside of the cell is called the membrane potential.

A neuron at rest is negatively charged: the inside of a cell is approximately 70 millivolts more negative than the outside (-70 mV). This voltage is called the resting membrane potential; it is caused by differences in the concentrations of ions inside and outside the cell and the selective permeability created by ion channels. Sodium-potassium pumps in the membrane produce the different ion concentrations inside and outside of the cell by bringing in two K^+ ions and removing three Na^+ ions. The actions of this pump are costly: one molecule of ATP is used up for each turn. Up to 50 percent of a neuron's ATP is used in maintaining its membrane resting potential. Potassium ions (K^+), which are higher inside the cell, move fairly freely out of the neuron through potassium channels; this loss of positive charge produces a net negative charge inside the cell. Sodium ions (Na^+), which are low inside, have a driving force to enter but move less freely. Their channels are voltage dependent and will open when a slight change in the membrane potential triggers them.

A neuron can receive input from other neurons and, if this input is strong enough, send the signal to downstream neurons. Transmission of a signal between neurons is generally carried by a chemical, called a neurotransmitter, which diffuses from the axon of one neuron to the dendrite of a second neuron. When neurotransmitter molecules bind to receptors located on a neuron's dendrites, the neurotransmitter opens ion channels in the dendrite's plasma membrane. This opening allows sodium ions to enter the neuron and results in **depolarization** of the membrane—a decrease in the voltage across the neuron membrane. Once a signal is

received by the dendrite, it then travels passively to the cell body. A large enough signal from neurotransmitters will reach the axon. If it is strong enough (that is, if the **threshold of excitation**, a depolarization to around -60mV is reached), then depolarization creates a positive feedback loop: as more Na^+ ions enter the cell, the axon becomes further depolarized, opening even more sodium channels at further distances from the cell body. This will cause voltage dependent Na^+ channels further down the axon to open and more positive ions to enter the cell. In the axon, this “signal” will become a self-propagating brief reversal of the resting membrane potential called an **action potential**.

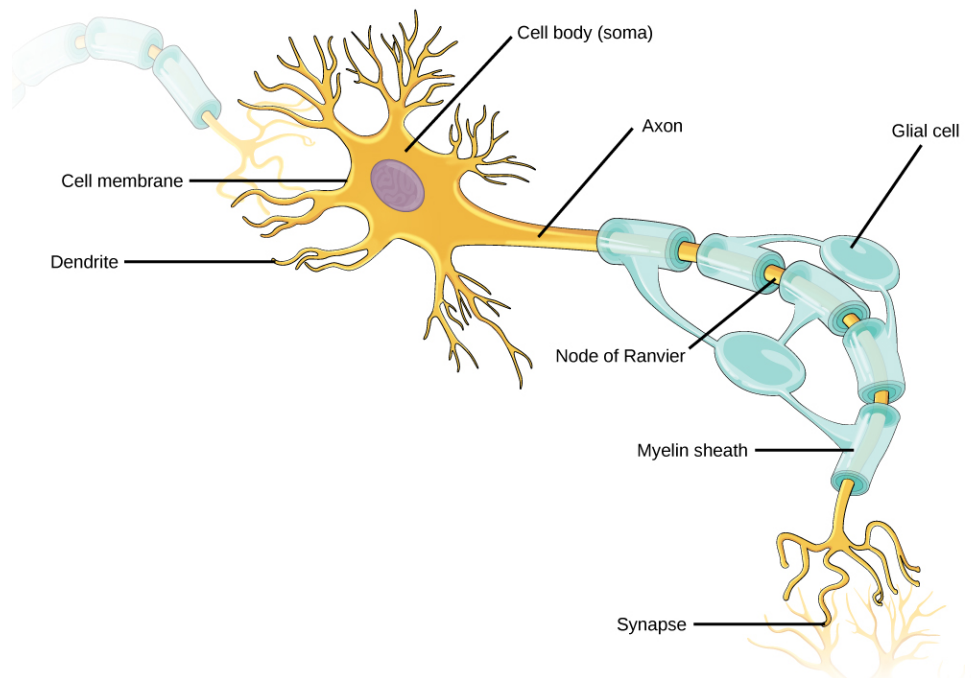
An action potential is an all-or-nothing event; it either happens or it does not. The threshold of excitation must be reached for the neuron to “fire” an action potential. As sodium ions rush into the cell, depolarization actually reverses the charge across the membrane from -70mV to $+30\text{mV}$. This change in the membrane potential causes voltage-gated K^+ channels to open, and K^+ begins to leave the cell, repolarizing it. At the same time, Na^+ channels inactivate so no more Na^+ enters the cell. K^+ ions continue to leave the cell and the membrane potential returns to the resting potential. At the resting potential, the K^+ channels close and Na^+ channels reset. The depolarization of the membrane proceeds in a wave down the length of the axon. It travels in only one direction because the sodium channels have been inactivated and unavailable until the membrane potential is near the resting potential again; at this point they are reset to closed and can be opened again.

An **axon** is a tube-like structure that propagates the signal from the cell body to specialized endings called axon terminals. These terminals in turn then synapse with other neurons, muscle, or target organs. When the action potential reaches the axon terminal, this causes the release of neurotransmitter onto the dendrite of another neuron. Neurotransmitters released at axon terminals allow signals to be communicated to these other cells, and the process begins again. Neurons usually have one or two axons, but some neurons do not contain any axons.

Some axons are covered with a special structure called a **myelin sheath**, which acts as an insulator to keep the electrical signal from dissipating as it

travels down the axon. This insulation is important, as the axon from a human motor neuron can be as long as a meter (3.2 ft)—from the base of the spine to the toes. The myelin sheath is produced by glial cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called nodes of Ranvier and are sites where the signal is “recharged” as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

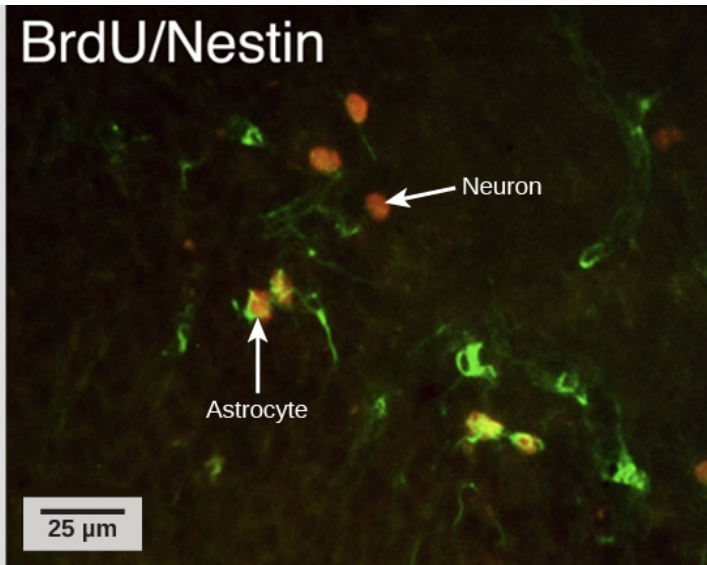


Neurons contain organelles common to other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Note:**Biology in Action****Neurogenesis**

At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1,000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of BrdU, and thus new neurons, in brain tissue ([link](#)).



This image shows new neurons in a rat hippocampus. New neurons tagged with BrdU glow red in this micrograph. (credit: modification of work by Dr. Maryam Faiz, University of Barcelona)

Note:

Concept in Action



Visit this link [interactive lab](#) to see more information about neurogenesis, including an interactive laboratory simulation and a video that explains how BrdU labels new cells.

While glial cells are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of 10. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

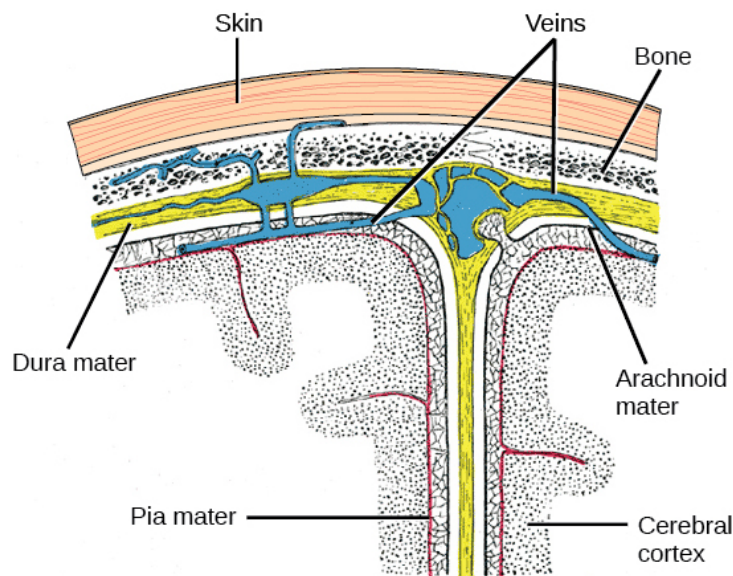
How Neurons Communicate

All functions performed by the nervous system—from a simple motor reflex to more advanced functions like making a memory or a decision—require neurons to communicate with one another. Neurons communicate between the axon of one neuron and the dendrites, and sometimes the cell body, of another neuron across the gap between them, known as the **synaptic cleft**. When an action potential reaches the end of an axon it stimulates the release of neurotransmitter molecules into the synaptic cleft between the synaptic knob of the axon and the post-synaptic membrane of the dendrite or soma of the next cell. The neurotransmitter is released through exocytosis of vesicles containing the neurotransmitter molecules. The neurotransmitter diffuses across the synaptic cleft and binds to receptors in the post-synaptic membrane. These receptor molecules are chemically regulated ion channels and will open, allowing sodium to enter the cell. If sufficient neurotransmitter has been released an action potential may be initiated in the next cell, but this is not guaranteed. If insufficient neurotransmitter is released the nerve signal will die at this point. There are a number of different neurotransmitters that are specific to neuron types that have specific functions.

The Central Nervous System

The **central nervous system (CNS)** is made up of the brain and spinal cord and is covered with three layers of protective coverings called **meninges** (“meninges” is derived from the Greek and means “membranes”) ([\[link\]](#)). The outermost layer is the dura mater, the middle layer is the web-like

arachnoid mater, and the inner layer is the pia mater, which directly contacts and covers the brain and spinal cord. The space between the arachnoid and pia maters is filled with **cerebrospinal fluid (CSF)**. The brain floats in CSF, which acts as a cushion and shock absorber.



The cerebral cortex is covered by three layers of meninges: the dura, arachnoid, and pia maters. (credit: modification of work by Gray's Anatomy)

The Brain

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, cerebellum, brainstem, and retinas. The outermost part of the brain is a thick piece of nervous system tissue called the **cerebral cortex**. The cerebral cortex, limbic system, and basal ganglia make up the two cerebral hemispheres. A thick fiber bundle called

the **corpus callosum** (corpus = “body”; callosum = “tough”) connects the two hemispheres. Although there are some brain functions that are localized more to one hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have very immature nervous systems.

In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients’ left visual field, they may be unable to verbally name the object (and may claim to not have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and cannot then signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of objects with the left hand, the patient will be able to do so but will still be unable to verbally identify it.

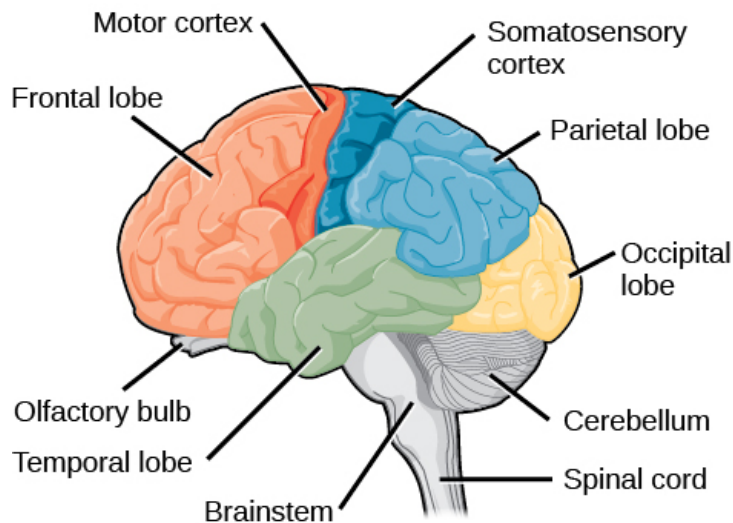
Note:

Concept in Action



Visit the following [website](#) to learn more about split-brain patients and to play a game where you can model split-brain experiments yourself.

Each hemisphere contains regions called lobes that are involved in different functions. Each hemisphere of the mammalian cerebral cortex can be broken down into four functionally and spatially defined lobes: frontal, parietal, temporal, and occipital ([\[link\]](#)).



The human cerebral cortex includes the frontal, parietal, temporal, and occipital lobes.

The **frontal lobe** is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups. Neurons in the frontal lobe also control cognitive functions like maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk. The **parietal lobe** is located at the top of the brain. Neurons in the parietal lobe are involved in speech and also reading. Two of the parietal lobe's main functions are processing somatosensation—touch sensations like pressure, pain, heat, cold—and processing proprioception—the sense of how parts of the body

are oriented in space. The parietal lobe contains a somatosensory map of the body similar to the motor cortex. The **occipital lobe** is located at the back of the brain. It is primarily involved in vision—seeing, recognizing, and identifying the visual world. The **temporal lobe** is located at the base of the brain and is primarily involved in processing and interpreting sounds. It also contains the **hippocampus** (named from the Greek for “seahorse,” which it resembles in shape) a structure that processes memory formation. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

Interconnected brain areas called the **basal ganglia** play important roles in movement control and posture. The basal ganglia also regulate motivation.

The **thalamus** acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states.

Below the thalamus is the **hypothalamus**. The hypothalamus controls the endocrine system by sending signals to the pituitary gland. Among other functions, the hypothalamus is the body’s thermostat—it makes sure the body temperature is kept at appropriate levels. Neurons within the hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

The **limbic system** is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the **amygdala**. The two amygdala (one on each side) are important both for the sensation of fear and for recognizing fearful faces.

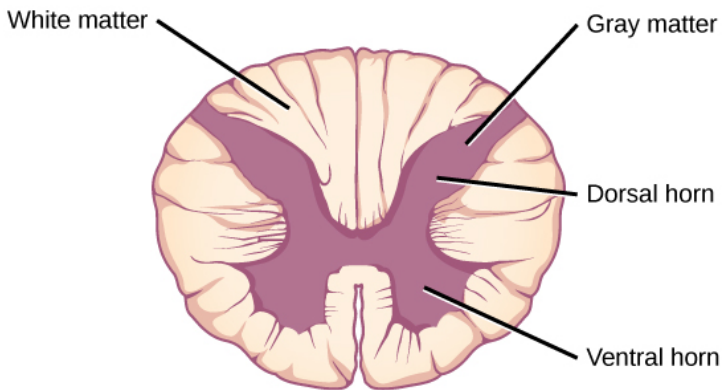
The **cerebellum** (cerebellum = “little brain”) sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks. The cerebellum of birds is large compared to other vertebrates because of the coordination required by flight.

The **brainstem** connects the rest of the brain with the spinal cord and regulates some of the most important and basic functions of the nervous system including breathing, swallowing, digestion, sleeping, walking, and sensory and motor information integration.

Spinal cord

Connecting to the brainstem and extending down the body through the spinal column is the spinal cord. The spinal cord is a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the meninges and the bones of the vertebral column but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape ([\[link\]](#)). Axons make up the “white matter” and neuron and glia cell bodies (and interneurons) make up the “gray matter.” Axons and cell bodies in the dorsal spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the spinal cord primarily transmit signals controlling movement from the brain to the body.

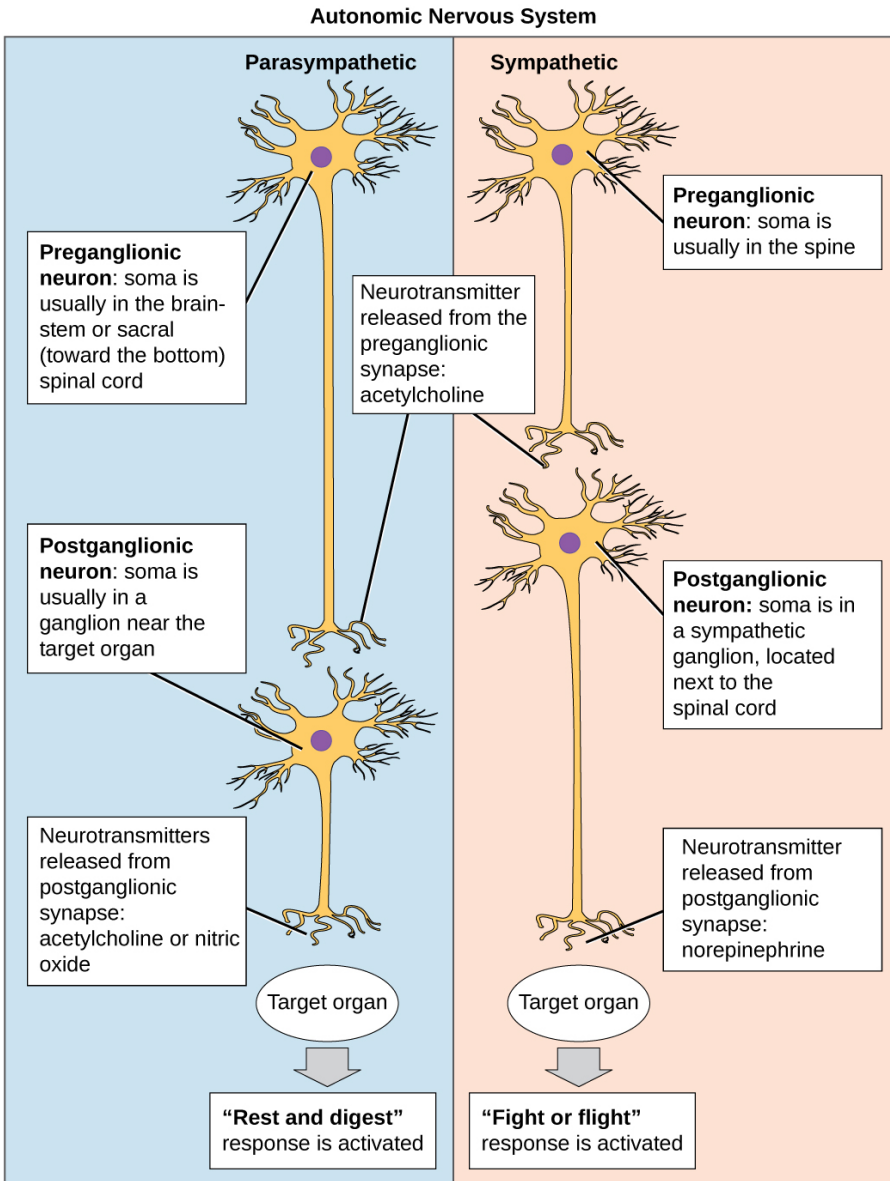
The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements—like automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).



A cross-section of the spinal cord shows gray matter (containing cell bodies and interneurons) and white matter (containing myelinated axons).

The Peripheral Nervous System

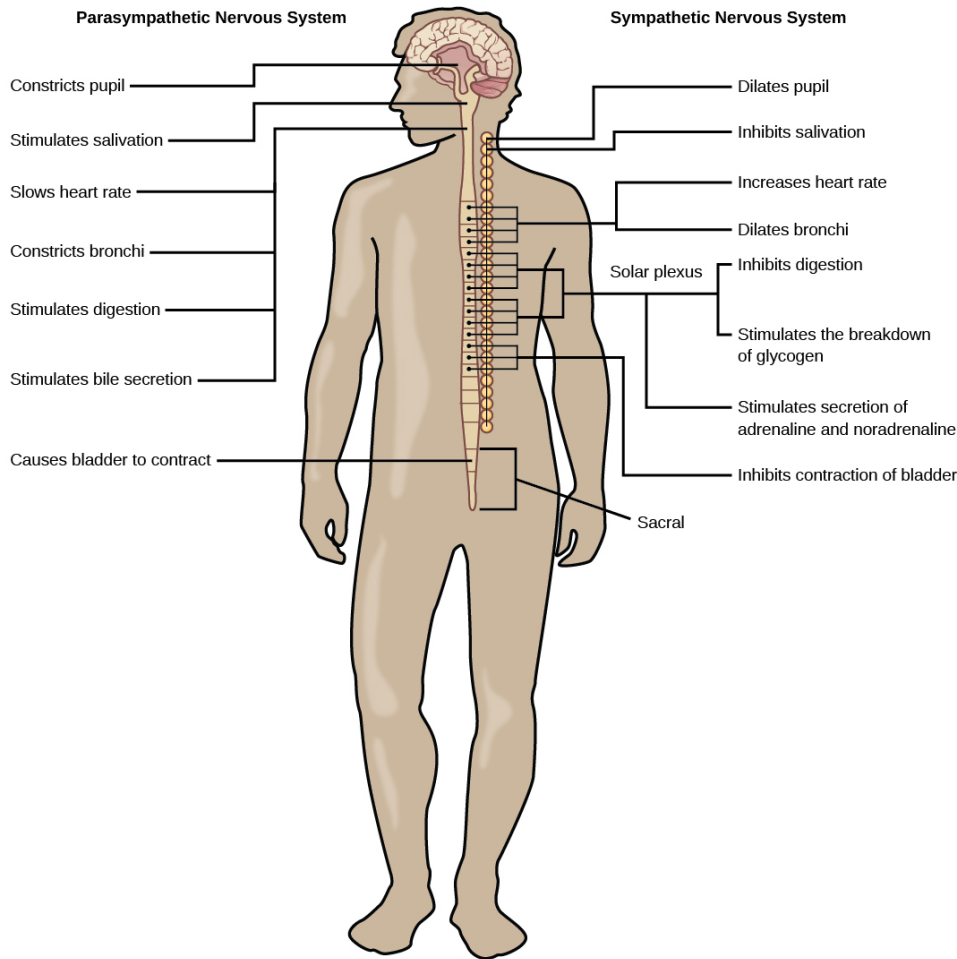
The **peripheral nervous system (PNS)** is the connection between the central nervous system and the rest of the body. The PNS can be broken down into the **autonomic nervous system**, which controls bodily functions without conscious control, and the **sensory-somatic nervous system**, which transmits sensory information from the skin, muscles, and sensory organs to the CNS and sends motor commands from the CNS to the muscles.



In the autonomic nervous system, a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on a target organ. Activation of the sympathetic nervous system causes release of norepinephrine on the target organ. Activation of the parasympathetic nervous system causes release of acetylcholine on the target organ.

The autonomic nervous system serves as the relay between the CNS and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands. The autonomic nervous system controls these organs largely without conscious control; it can continuously monitor the conditions of these different systems and implement changes as needed. Signaling to the target tissue usually involves two synapses: a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ ([link](#)). There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

The **sympathetic nervous system** is responsible for the immediate responses an animal makes when it encounters a dangerous situation. One way to remember this is to think of the “fight-or-flight” response a person feels when encountering a snake (“snake” and “sympathetic” both begin with “s”). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion. These functions help prepare an organism’s body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.



The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

While the sympathetic nervous system is activated in stressful situations, the **parasympathetic nervous system** allows an animal to “rest and digest.” One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control (“picnic” and “parasympathetic” both start with “p”). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord ([link](#)). The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated including slowing of heart rate, lowered blood pressure, and stimulation of digestion.

The sensory-somatic nervous system is made up of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the CNS. Motor neurons transmit messages about desired movement from the CNS to the muscles to make them contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, and so on) and could not control motor movements. Unlike the autonomic nervous system, which usually has two synapses between the CNS and the target organ, sensory and motor neurons usually have only one synapse—one ending of the neuron is at the organ and the other directly contacts a CNS neuron.

Section Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

Neurons have a resting potential across their membranes and when they are stimulated by a strong enough signal from another neuron an action potential may carry an electrochemical signal along the neuron to a synapse with another neuron. Neurotransmitters carry signals across synapses to initiate a response in another neuron.

The vertebrate central nervous system contains the brain and the spinal cord, which are covered and protected by three meninges. The brain contains structurally and functionally defined regions. In mammals, these include the cortex (which can be broken down into four primary functional lobes: frontal, temporal, occipital, and parietal), basal ganglia, thalamus, hypothalamus, limbic system, cerebellum, and brainstem—although structures in some of these designations overlap. While functions may be primarily localized to one structure in the brain, most complex functions, like language and sleep, involve neurons in multiple brain regions. The spinal cord is the information superhighway that connects the brain with the

rest of the body through its connections with peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

The peripheral nervous system contains both the autonomic and sensory-somatic nervous systems. The autonomic nervous system provides unconscious control over visceral functions and has two divisions: the sympathetic and parasympathetic nervous systems. The sympathetic nervous system is activated in stressful situations to prepare the animal for a “fight-or-flight” response. The parasympathetic nervous system is active during restful periods. The sensory-somatic nervous system is made of cranial and spinal nerves that transmit sensory information from skin and muscle to the CNS and motor commands from the CNS to the muscles.

Review Questions

Exercise:

Problem:

Neurons contain _____, which can receive signals from other neurons.

- a. axons
- b. mitochondria
- c. dendrites
- d. Golgi bodies

Solution:

C

Exercise:

Problem:

The part of the brain that is responsible for coordination during movement is the _____.

- a. limbic system
 - b. thalamus
 - c. cerebellum
 - d. parietal lobe
-

Solution:

C

Exercise:

Problem:

Which part of the nervous system directly controls the digestive system?

- a. parasympathetic nervous system
 - b. central nervous system
 - c. spinal cord
 - d. sensory-somatic nervous system
-

Solution:

A

Free Response

Exercise:

Problem:

How are neurons similar to other cells? How are they unique?

Solution:

Neurons contain organelles common to all cells, such as a nucleus and mitochondria. They are unique because they contain dendrites, which

can receive signals from other neurons, and axons that can send these signals to other cells.

Exercise:

Problem:What are the main functions of the spinal cord?

Solution:

The spinal cord transmits sensory information from the body to the brain and motor commands from the brain to the body through its connections with peripheral nerves. It also controls motor reflexes.

Exercise:

Problem:

What are the main differences between the sympathetic and parasympathetic branches of the autonomic nervous system?

Solution:

The sympathetic nervous system prepares the body for “fight or flight,” whereas the parasympathetic nervous system allows the body to “rest and digest.” Sympathetic neurons release norepinephrine onto target organs; parasympathetic neurons release acetylcholine. Sympathetic neuron cell bodies are located in sympathetic ganglia. Parasympathetic neuron cell bodies are located in the brainstem and sacral spinal cord. Activation of the sympathetic nervous system increases heart rate and blood pressure and decreases digestion and blood flow to the skin. Activation of the parasympathetic nervous system decreases heart rate and blood pressure and increases digestion and blood flow to the skin.

Exercise:

Problem:

What are the main functions of the sensory-somatic nervous system?

Solution:

The sensory-somatic nervous system transmits sensory information from the skin, muscles, and sensory organs to the CNS. It also sends motor commands from the CNS to the muscles, causing them to contract.

Glossary

action potential

a momentary change in the electrical potential of a neuron (or muscle) membrane

amygdala

a structure within the limbic system that processes fear

autonomic nervous system

the part of the peripheral nervous system that controls bodily functions

axon

a tube-like structure that propagates a signal from a neuron's cell body to axon terminals

basal ganglia

an interconnected collections of cells in the brain that are involved in movement and motivation

brainstem

a portion of brain that connects with the spinal cord; controls basic nervous system functions like breathing and swallowing

central nervous system (CNS)

the nervous system made up of the brain and spinal cord; covered with three layers of protective meninges

cerebellum

the brain structure involved in posture, motor coordination, and learning new motor actions

cerebral cortex

the outermost sheet of brain tissue; involved in many higher-order functions

cerebrospinal fluid (CSF)

a clear liquid that surrounds the brain and fills its ventricles and acts as a shock absorber

corpus callosum

a thick nerve bundle that connects the cerebral hemispheres

dendrite

a structure that extends away from the cell body to receive messages from other neurons

depolarization

a change in the membrane potential to a less negative value

frontal lobe

the part of the cerebral cortex that contains the motor cortex and areas involved in planning, attention, and language

glia

(also, glial cells) the cells that provide support functions for neurons

hippocampus

the brain structure in the temporal lobe involved in processing memories

hypothalamus

the brain structure that controls hormone release and body homeostasis

limbic system

a connected brain area that processes emotion and motivation

membrane potential

a difference in electrical potential between the inside and outside of a cell

meninges

(singular: meninx) the membranes that cover and protect the central nervous system

myelin sheath

a cellular extension containing a fatty substance produced by glia that surrounds and insulates axons

neuron

a specialized cell that can receive and transmit electrical and chemical signals

occipital lobe

the part of the cerebral cortex that contains visual cortex and processes visual stimuli

parasympathetic nervous system

the division of autonomic nervous system that regulates visceral functions during relaxation

parietal lobe

the part of the cerebral cortex involved in processing touch and the sense of the body in space

peripheral nervous system (PNS)

the nervous system that serves as the connection between the central nervous system and the rest of the body; consists of the autonomic nervous system and the sensory-somatic nervous system

sensory-somatic nervous system

the system of sensory and motor nerves

spinal cord

a thick fiber bundle that connects the brain with peripheral nerves; transmits sensory and motor information; contains neurons that control

motor reflexes

sympathetic nervous system

the division of autonomic nervous system activated during stressful "fight-or-flight" situations

synapse

a junction between two neurons where neuronal signals are communicated

synaptic cleft

a space between the presynaptic and postsynaptic membranes

temporal lobe

the part of the cerebral cortex that processes auditory input; parts of the temporal lobe are involved in speech, memory, and emotion processing

thalamus

the brain area that relays sensory information to the cortex

threshold of excitation

the level of depolarization needed for an action potential to fire

Introduction

class="introduction"

(a) This
smallpox
(variola)
vaccine is
derived
from calves
exposed to
cowpox
virus.

Vaccines
provoke a
reaction in
the immune
system that
prepares it
for a
subsequent
infection by
smallpox.

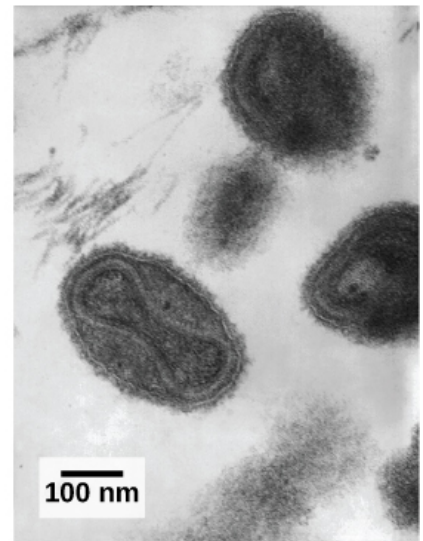
(b) Viewed
under a
transmission
electron
microscope,
you can see
the variola's
dumbbell-
shaped
structure
that contains
the viral
DNA.

(credit a:
modificatio

n of work
by James
Gathany,
CDC; credit
b:
modificatio
n of work
by Dr. Fred
Murphy;
Sylvia
Whitfield,
CDC; scale-
bar data
from Matt
Russell)



(a)



(b)

Organisms have a wide array of adaptations for preventing attacks of parasites and diseases. The vertebrate defense systems, including those of humans, are complex and multilayered, with defenses unique to vertebrates. These unique vertebrate defenses interact with other defense systems inherited from ancestral lineages, and include complex and specific

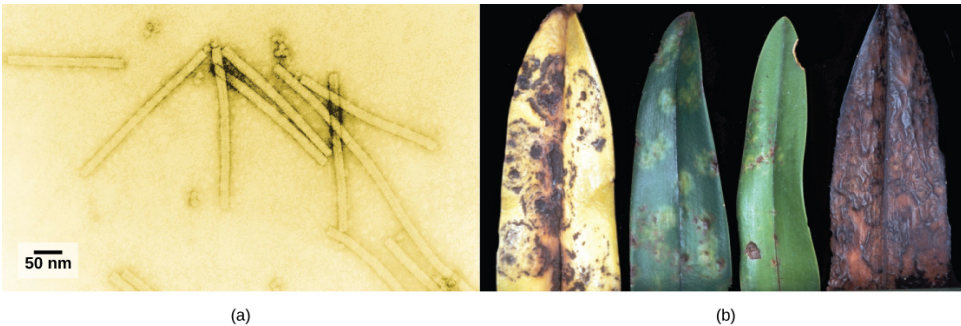
pathogen recognition and memory mechanisms. Research continues to unravel the complexities and vulnerabilities of the immune system.

Despite a poor understanding of the workings of the body in the early 18th century in Europe, the practice of inoculation as a method to prevent the often-deadly effects of smallpox was introduced from the courts of the Ottoman Empire. The method involved causing limited infection with the smallpox virus by introducing the pus of an affected individual to a scratch in an uninfected person. The resulting infection was milder than if it had been caught naturally and mortality rates were shown to be about two percent rather than 30 percent from natural infections. Moreover, the inoculation gave the individual immunity to the disease. It was from these early experiences with inoculation that the methods of vaccination were developed, in which a weakened or relatively harmless (killed) derivative of a pathogen is introduced into the individual. The vaccination induces immunity to the disease with few of the risks of being infected. A modern understanding of the causes of the infectious disease and the mechanisms of the immune system began in the late 19th century and continues to grow today.

Viruses

By the end of this section, you will be able to:

- Describe how viruses were first discovered and how they are detected
- Explain the detailed steps of viral replication
- Describe how vaccines are used in prevention and treatment of viral diseases



(a) The tobacco mosaic virus, seen by transmission electron microscopy, was the first virus to be discovered. (b) The leaves of an infected plant are shown. (credit a: scale-bar data from Matt Russell; credit b: modification of work by USDA, Department of Plant Pathology Archive, North Carolina State University)

No one knows exactly when viruses emerged or from where they came, since viruses do not leave historical footprints such as fossils. Modern viruses are thought to be a mosaic of bits and pieces of nucleic acids picked up from various sources along their respective evolutionary paths. Viruses are **acellular**, parasitic entities that are not classified within any domain because they are not considered alive. They have no plasma membrane, internal organelles, or metabolic processes, and they do not divide. Instead, they infect a host cell and use the host's replication processes to produce progeny virus particles. Viruses infect all forms of organisms including bacteria, archaea, fungi, plants, and animals. Living things grow, metabolize, and reproduce. Viruses replicate, but to do so, they are entirely

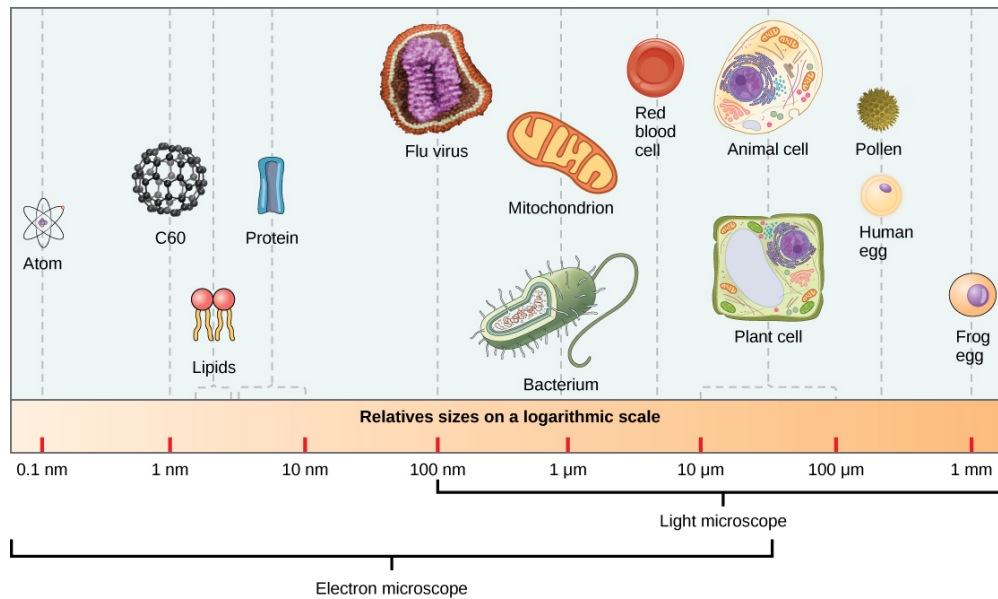
dependent on their host cells. They do not metabolize or grow, but are assembled in their mature form.

Viruses are diverse. They vary in their structure, their replication methods, and in their target hosts or even host cells. While most biological diversity can be understood through evolutionary history, such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown.

How Viruses Replicate

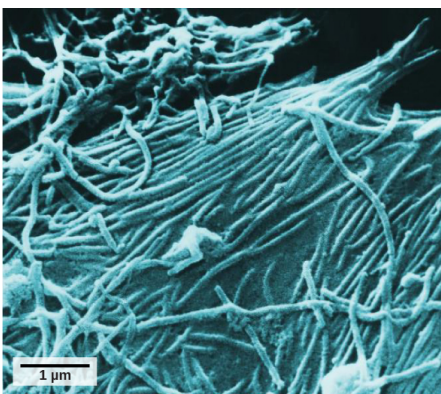
Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible under the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one through liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these “filterable” infectious agents were not simply very small bacteria but were a new type of tiny, disease-causing particle.

Virions, single virus particles, are very small, about 20–250 nanometers (1 nanometer = 1/1,000,000 mm). These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100 times larger), we cannot see viruses with a light microscope, with the exception of some large virions of the poxvirus family ([\[link\]](#)).

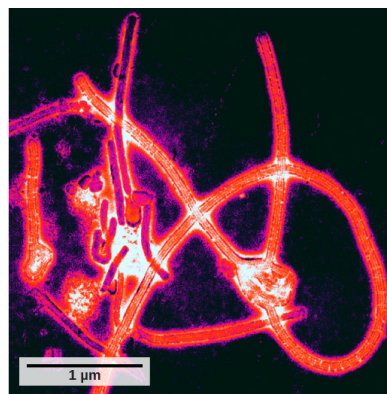


The size of a virus is very small relative to the size of cells and organelles.

It was not until the development of the electron microscope in the 1940s that scientists got their first good view of the structure of the tobacco mosaic virus ([\[link\]](#)) and others. The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope ([\[link\]](#)).



(a)



(b)

The ebola virus is shown here as visualized through (a) a scanning electron micrograph and (b) a transmission electron micrograph. (credit a: modification of work by Cynthia Goldsmith, CDC; credit b: modification of work by Thomas W. Geisbert, Boston University School of Medicine; scale-bar data from Matt Russell)

The use of this technology has allowed for the discovery of many viruses of all types of living organisms. They were initially grouped by shared morphology, meaning their size, shape, and distinguishing structures. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replication cycles has further refined their classification.

A **virion** consists of a nucleic-acid core, an outer protein coating, and sometimes an outer envelope made of protein and phospholipid membranes derived from the host cell. The most visible difference between members of viral families is their morphology, which is quite diverse. An interesting feature of viral complexity is that the complexity of the host does not correlate to the complexity of the virion. Some of the most complex virion structures are observed in bacteriophages, viruses that infect the simplest living organisms, bacteria.

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family ([link](#)). All virions have a nucleic-acid genome covered by a protective layer of protein, called a **capsid**. The capsid is made of protein subunits called capsomeres. Some viral capsids are simple polyhedral “spheres,” whereas others are quite complex in structure. The outer structure surrounding the capsid of some viruses is called the **viral envelope**. All viruses use some sort of **glycoprotein** to attach to their host cells at molecules on the cell called viral receptors. The virus exploits these cell-surface molecules, which the cell uses for some other purpose, as a way

to recognize and infect specific cell types. For example, the measles virus uses a cell-surface glycoprotein in humans that normally functions in immune reactions and possibly in the sperm-egg interaction at fertilization. Attachment is a requirement for viruses to later penetrate the cell membrane, inject the viral genome, and complete their replication inside the cell.

The T4 bacteriophage, which infects the *E. coli* bacterium, is among the most complex virion known; T4 has a protein tail structure that the virus uses to attach to the host cell and a head structure that houses its DNA.

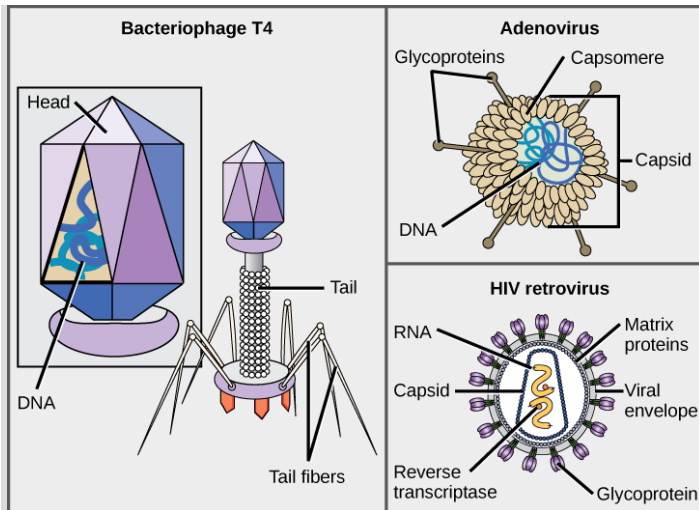
Adenovirus, a nonenveloped animal virus that causes respiratory illnesses in humans, uses protein spikes protruding from its capsomeres to attach to the host cell. Nonenveloped viruses also include those that cause polio (poliovirus), plantar warts (papillomavirus), and hepatitis A (hepatitis A virus). Nonenveloped viruses tend to be more robust and more likely to survive under harsh conditions, such as the gut.

Enveloped virions like HIV (human immunodeficiency virus), the causative agent in AIDS (acquired immune deficiency syndrome), consist of nucleic acid (RNA in the case of HIV) and capsid proteins surrounded by a phospholipid bilayer envelope and its associated proteins ([\[link\]](#)). Chicken pox, influenza, and mumps are examples of diseases caused by viruses with envelopes. Because of the fragility of the envelope, nonenveloped viruses are more resistant to changes in temperature, pH, and some disinfectants than enveloped viruses.

Overall, the shape of the virion and the presence or absence of an envelope tells us little about what diseases the viruses may cause or what species they might infect, but is still a useful means to begin viral classification.

Note:

Art Connection



Viruses can be complex in shape or relatively simple. This figure shows three relatively complex virions: the bacteriophage T4, with its DNA-containing head group and tail fibers that attach to host cells; adenovirus, which uses spikes from its capsid to bind to the host cells; and HIV, which uses glycoproteins embedded in its envelope to do so. Notice that HIV has proteins called matrix proteins, internal to the envelope, which help stabilize virion shape. HIV is a retrovirus, which means it reverse transcribes its RNA genome into DNA, which is then spliced into the host's DNA. (credit "bacteriophage, adenovirus": modification of work by NCBI, NIH; credit "HIV retrovirus": modification of work by NIAID, NIH)

Which of the following statements about virus structure is true?

- All viruses are encased in a viral membrane.

- b. The capsomere is made up of small protein subunits called capsids.
- c. DNA is the genetic material in all viruses.
- d. Glycoproteins help the virus attach to the host cell.

Unlike all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA as theirs. The virus core contains the genome or total genetic content of the virus. Viral genomes tend to be small compared to bacteria or eukaryotes, containing only those genes that code for proteins the virus cannot get from the host cell. This genetic material may be single-stranded or double-stranded. It may also be linear or circular. While most viruses contain a single segment of nucleic acid, others have genomes that consist of several segments.

DNA viruses have a DNA core. The viral DNA directs the host cell's replication proteins to synthesize new copies of the viral genome and to transcribe and translate that genome into viral proteins. DNA viruses cause human diseases such as chickenpox, hepatitis B, and some venereal diseases like herpes and genital warts.

RNA viruses contain only RNA in their cores. To replicate their genomes in the host cell, the genomes of RNA viruses encode enzymes not found in host cells. RNA polymerase enzymes are not as stable as DNA polymerases and often make mistakes during transcription. For this reason, mutations, changes in the nucleotide sequence, in RNA viruses occur more frequently than in DNA viruses. This leads to more rapid evolution and change in RNA viruses. For example, the fact that influenza is an RNA virus is one reason a new flu vaccine is needed every year. Human diseases caused by RNA viruses include hepatitis C, measles, and rabies.

Viruses can be seen as obligate intracellular parasites. The virus must attach to a living cell, be taken inside, manufacture its proteins and copy its genome, and find a way to escape the cell so the virus can infect other cells and ultimately other individuals. Viruses can infect only certain species of hosts and only certain cells within that host. The molecular basis for this specificity is that a particular surface molecule, known as the viral receptor,

must be found on the host cell surface for the virus to attach. Also, metabolic differences seen in different cell types based on differential gene expression are a likely factor in which cells a virus may use to replicate. The cell must be making the substances the virus needs, such as enzymes the virus genome itself does not have genes for, or the virus will not be able to replicate using that cell.

Steps of Virus Infections

A virus must “take over” a cell to replicate. The viral replication cycle can produce dramatic biochemical and structural changes in the host cell, which may cause cell damage. These changes, called **cytopathic** effects, can change cell functions or even destroy the cell. Some infected cells, such as those infected by the common cold virus (rhinovirus), die through lysis (bursting) or **apoptosis** (programmed cell death or “cell suicide”), releasing all the progeny virions at once. The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body, and from cell damage caused by the virus. Many animal viruses, such as HIV (human immunodeficiency virus), leave the infected cells of the immune system by a process known as budding, where virions leave the cell individually. During the budding process, the cell does not undergo lysis and is not immediately killed. However, the damage to the cells that HIV infects may make it impossible for the cells to function as mediators of immunity, even though the cells remain alive for a period of time. Most productive viral infections follow similar steps in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release.

A virus attaches to a specific receptor site on the host-cell membrane through attachment proteins in the capsid or proteins embedded in its envelope. The attachment is specific, and typically a virus will only attach to cells of one or a few species and only certain cell types within those species with the appropriate receptors.

Note:

Concept in Action



View this [video](#) for a visual explanation of how influenza attacks the body.

Unlike animal viruses, the nucleic acid of bacteriophages is injected into the host cell naked, leaving the capsid outside the cell. Plant and animal viruses can enter their cells through endocytosis, in which the cell membrane surrounds and engulfs the entire virus. Some enveloped viruses enter the cell when the viral envelope fuses directly with the cell membrane. Once inside the cell, the viral capsid is degraded and the viral nucleic acid is released, which then becomes available for replication and transcription.

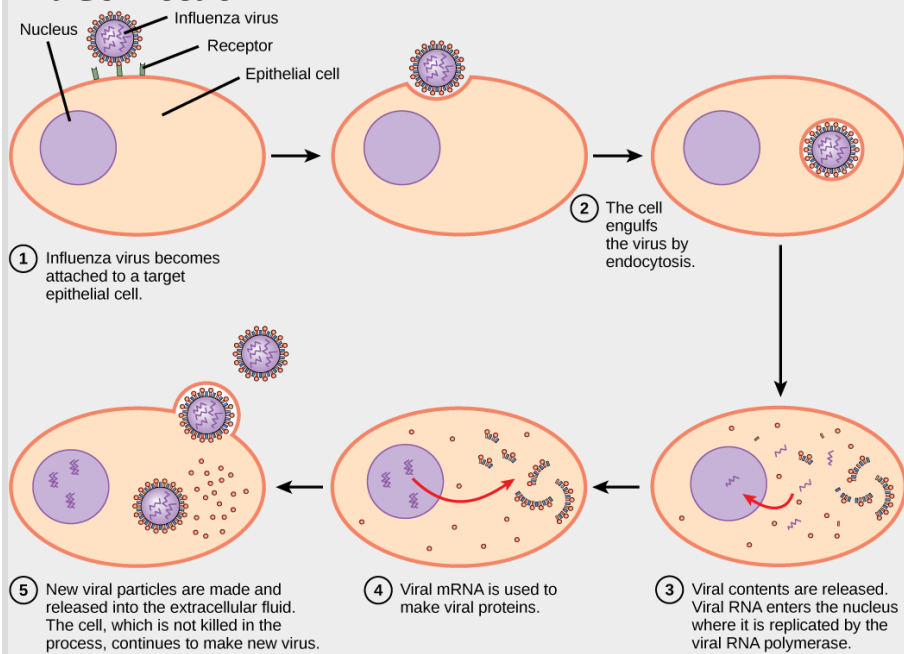
The replication mechanism depends on the viral genome. DNA viruses usually use host cell proteins and enzymes to make additional DNA that is used to copy the genome or be transcribed to messenger RNA (mRNA), which is then used in protein synthesis. RNA viruses, such as the influenza virus, usually use the RNA core as a template for synthesis of viral genomic RNA and mRNA. The viral mRNA is translated into viral enzymes and capsid proteins to assemble new virions ([\[link\]](#)). Of course, there are exceptions to this pattern. If a host cell does not provide the enzymes necessary for viral replication, viral genes supply the information to direct synthesis of the missing proteins. Retroviruses, such as HIV, have an RNA genome that must be reverse transcribed to make DNA, which then is inserted into the host's DNA. To convert RNA into DNA, retroviruses contain genes that encode the virus-specific enzyme reverse transcriptase that transcribes an RNA template to DNA. The fact that HIV produces some of its own enzymes, which are not found in the host, has allowed researchers to develop drugs that inhibit these enzymes. These drugs,

including the reverse transcriptase inhibitor AZT, inhibit HIV replication by reducing the activity of the enzyme without affecting the host's metabolism.

The last stage of viral replication is the release of the new virions into the host organism, where they are able to infect adjacent cells and repeat the replication cycle. Some viruses are released when the host cell dies and other viruses can leave infected cells by budding through the membrane without directly killing the cell.

Note:

Art Connection



In influenza virus infection, glycoproteins attach to a host epithelial cell. As a result, the virus is engulfed. RNA and proteins are made and assembled into new virions.

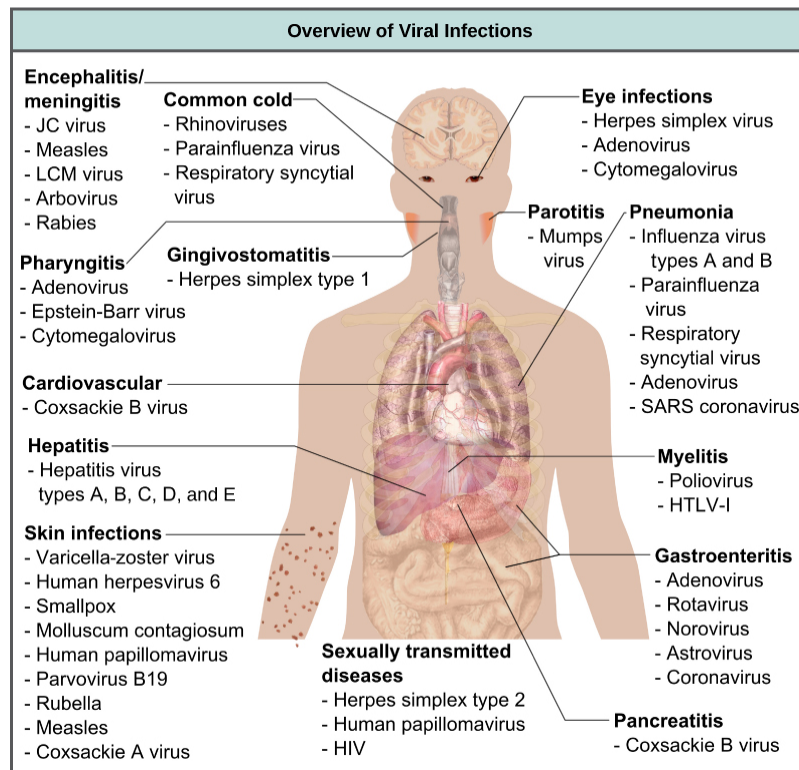
Influenza virus is packaged in a viral envelope, which fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Note:**Concept in Action**

Click through this [tutorial](#) on viruses to identify structures, modes of transmission, replication, and more.

Viruses and Disease

Viruses cause a variety of diseases in animals, including humans, ranging from the common cold to potentially fatal illnesses like meningitis ([link](#)). These diseases can be treated by antiviral drugs or by vaccines, but some viruses, such as HIV, are capable of avoiding the immune response and mutating so as to become resistant to antiviral drugs.



Viruses are the cause of dozens of ailments in humans, ranging from mild illnesses to serious diseases. (credit: modification of work by Mikael Häggström)

Vaccines for Prevention

While we do have limited numbers of effective antiviral drugs, such as those used to treat HIV and influenza, the primary method of controlling viral disease is by vaccination, which is intended to prevent outbreaks by building immunity to a virus or virus family. A **vaccine** may be prepared using weakened live viruses, killed viruses, or molecular subunits of the virus. In general, live viruses lead to better immunity, but have the possibility of causing disease at some low frequency. Killed viral vaccine and the subunit viruses are both incapable of causing disease, but in general lead to less effective or long-lasting immunity.

Weakened live viral vaccines are designed in the laboratory to cause few symptoms in recipients while giving them immunity against future infections. Polio was one disease that represented a milestone in the use of vaccines. Mass immunization campaigns in the U.S. in the 1950s (killed vaccine) and 1960s (live vaccine) essentially eradicated the disease, which caused muscle paralysis in children and generated fear in the general population when regional epidemics occurred. The success of the polio vaccine paved the way for the routine dispensation of childhood vaccines against measles, mumps, rubella, chickenpox, and other diseases.

Live vaccines are usually made by **attenuation** (weakening) of the “wild-type” (disease-causing) virus by growing it in the laboratory in tissues or at temperatures different from what the virus is accustomed to in the host. For example, the virus may be grown in cells in a test tube, in bird embryos, or in live animals. The adaptation to these new cells or temperature induces mutations in the virus’ genomes, allowing them to grow better in the laboratory while inhibiting their ability to cause disease when reintroduced into the conditions found in the host. These attenuated viruses thus still cause an infection, but they do not grow very well, allowing the immune response to develop in time to prevent major disease. The danger of using live vaccines, which are usually more effective than killed vaccines, is the low but significant risk that these viruses will revert back to their disease-causing form by back mutations. Back mutations occur when the vaccine undergoes mutations in the host such that it readapts to the host and can again cause disease, which can then be spread to other humans in an epidemic. This happened as recently as 2007 in Nigeria where mutations in a polio vaccine led to an epidemic of polio in that country.

Some vaccines are in continuous development because certain viruses, such as influenza and HIV, have a high mutation rate compared to other viruses or host cells. With influenza, mutation in genes for the surface molecules helps the virus evade the protective immunity that may have been obtained in a previous influenza season, making it necessary for individuals to get vaccinated every year. Other viruses, such as those that cause the childhood diseases measles, mumps, and rubella, mutate so little that the same vaccine is used year after year.

Vaccines and Antiviral Drugs for Treatment

In some cases, vaccines can be used to treat an active viral infection. In the case of rabies, a fatal neurological disease transmitted in the saliva of rabies virus-infected animals, the progression of the disease from the time of the animal bite to the time it enters the central nervous system may be two weeks or longer. This is enough time to vaccinate an individual who suspects being bitten by a rabid animal, and the boosted immune response from the vaccination is enough to prevent the virus from entering nervous tissue. Thus, the fatal neurological consequences of the disease are averted and the individual only has to recover from the infected bite. This approach is also being used for the treatment of Ebola, one of the fastest and most deadly viruses affecting humans, though usually infecting limited populations. Ebola is also a leading cause of death in gorillas. Transmitted by bats and great apes, this virus can cause death in 70–90 percent of the infected within two weeks. Using newly developed vaccines that boost the immune response, there is hope that immune systems of affected individuals will be better able to control the virus, potentially reducing mortality rates.

Another way of treating viral infections is the use of antiviral drugs. These drugs often have limited ability to cure viral disease but have been used to control and reduce symptoms for a wide variety of viral diseases. For most viruses, these drugs inhibit the virus by blocking the actions of one or more of its proteins. It is important that the targeted proteins be encoded for by viral genes and that these molecules are not present in a healthy host cell. In this way, viral growth is inhibited without damaging the host. There are large numbers of antiviral drugs available to treat infections, some specific for a particular virus and others that can affect multiple viruses.

Antivirals have been developed to treat genital herpes (herpes simplex II) and influenza. For genital herpes, drugs such as acyclovir can reduce the number and duration of the episodes of active viral disease during which patients develop viral lesions in their skin cells. As the virus remains latent in nervous tissue of the body for life, this drug is not a cure but can make the symptoms of the disease more manageable. For influenza, drugs like Tamiflu can reduce the duration of “flu” symptoms by one or two days, but

the drug does not prevent symptoms entirely. Other antiviral drugs, such as Ribavirin, have been used to treat a variety of viral infections.

By far the most successful use of antivirals has been in the treatment of the retrovirus HIV, which causes a disease that, if untreated, is usually fatal within 10–12 years after being infected. Anti-HIV drugs have been able to control viral replication to the point that individuals receiving these drugs survive for a significantly longer time than the untreated.

Anti-HIV drugs inhibit viral replication at many different phases of the HIV replicative cycle. Drugs have been developed that inhibit the fusion of the HIV viral envelope with the plasma membrane of the host cell (fusion inhibitors), the conversion of its RNA genome to double-stranded DNA (reverse transcriptase inhibitors), the integration of the viral DNA into the host genome (integrase inhibitors), and the processing of viral proteins (protease inhibitors).

When any of these drugs are used individually, the virus' high mutation rate allows the virus to rapidly evolve resistance to the drug. The breakthrough in the treatment of HIV was the development of highly active anti-retroviral therapy (HAART), which involves a mixture of different drugs, sometimes called a drug “cocktail.” By attacking the virus at different stages of its replication cycle, it is difficult for the virus to develop resistance to multiple drugs at the same time. Still, even with the use of combination HAART therapy, there is concern that, over time, the virus will evolve resistance to this therapy. Thus, new anti-HIV drugs are constantly being developed with the hope of continuing the battle against this highly fatal virus.

Section Summary

Viruses are acellular entities that can usually only be seen with an electron microscope. Their genomes contain either DNA or RNA, and they replicate using the replication proteins of a host cell. Viruses are diverse, infecting archaea, bacteria, fungi, plants, and animals. Viruses consist of a nucleic-acid core surrounded by a protein capsid with or without an outer lipid envelope.

Viral replication within a living cell always produces changes in the cell, sometimes resulting in cell death and sometimes slowly killing the infected cells. There are six basic stages in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release. A viral infection may be productive, resulting in new virions, or nonproductive, meaning the virus remains inside the cell without producing new virions.

Viruses cause a variety of diseases in humans. Many of these diseases can be prevented by the use of viral vaccines, which stimulate protective immunity against the virus without causing major disease. Viral vaccines may also be used in active viral infections, boosting the ability of the immune system to control or destroy the virus. Antiviral drugs that target enzymes and other protein products of viral genes have been developed and used with mixed success. Combinations of anti-HIV drugs have been used to effectively control the virus, extending the lifespan of infected individuals.

Art Connections

Exercise:

Problem:

[\[link\]](#) Which of the following statements about virus structure is true?

- a. All viruses are encased in a viral membrane.
- b. The capsomere is made up of small protein subunits called capsids.
- c. DNA is the genetic material in all viruses.
- d. Glycoproteins help the virus attach to the host cell.

Solution:

[\[link\]](#) D

Exercise:

Problem:

[\[link\]](#) Influenza virus is packaged in a viral envelope, which fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Solution:

[\[link\]](#) The host cell can continue to make new virus particles.

Review Questions**Exercise:**

Problem: Which statement is true?

- a. A virion contains DNA and RNA.
 - b. Viruses are acellular.
 - c. Viruses replicate outside of the cell.
 - d. Most viruses are easily visualized with a light microscope.
-

Solution:

B

Exercise:**Problem:**

The viral _____ plays a role in attaching a virion to the host cell.

- a. core
- b. capsid
- c. envelope
- d. both b and c

Solution:

D

Exercise:

Problem: Which statement is true of viral replication?

- a. In the process of apoptosis, the cell survives.
- b. During attachment, the virus attaches at specific sites on the cell surface.
- c. The viral capsid helps the host cell produce more copies of the viral genome.
- d. mRNA works outside of the host cell to produce enzymes and proteins.

Solution:

B

Free Response**Exercise:**

Problem: Why can't dogs catch the measles?

Solution:

The virus cannot attach to dog cells because dog cells do not express the receptors for the virus or there is no cell within the dog that is permissive for viral replication.

Exercise:

Problem:

Why is immunization after being bitten by a rabid animal so effective?

Solution:

Rabies vaccine works after a bite because it takes two weeks for the virus to travel from the site of the bite to the central nervous system, where the most severe symptoms of the disease occur. The vaccine is able to cause an immune response in the body during this time that clears the infection before it reaches the nervous system.

Glossary

acellular

lacking cells

apoptosis

the cell death caused by induction of a cell's own internal mechanisms either as a natural step in the development of a multicellular organism or by other environmental factors such as signals from cells of the immune system

attenuation

the weakening of a virus during vaccine development

capsid

the protein coating of the viral core

cytopathic

causing cell damage

glycoprotein

a protein molecule with attached carbohydrate molecules

vaccine

a weakened solution of virus components, viruses, or other agents that produce an immune response

virion

an individual virus particle outside a host cell

viral envelope

a lipid bilayer that envelops some viruses

Innate Immunity

By the end of this section, you will be able to:

- Describe the body’s innate physical and chemical defenses
- Explain the inflammatory response
- Describe the complement system

The vertebrate, including human, immune system is a complex multilayered system for defending against external and internal threats to the integrity of the body. The system can be divided into two types of defense systems: the innate immune system, which is nonspecific toward a particular kind of pathogen, and the adaptive immune system, which is specific ([link](#)).

Innate immunity is not caused by an infection or vaccination and depends initially on physical and chemical barriers that work on all pathogens, sometimes called the first line of defense. The second line of defense of the innate system includes chemical signals that produce inflammation and fever responses as well as mobilizing protective cells and other chemical defenses. The adaptive immune system mounts a highly specific response to substances and organisms that do not belong in the body. The adaptive system takes longer to respond and has a memory system that allows it to respond with greater intensity should the body reencounter a pathogen even years later.

Vertebrate Immunity		
Innate Immune System		Adaptive Immune System
Physical Barriers	Internal Defenses	• Antibodies and the humoral immune response • Cell-mediated immune response • Memory response
• Skin, hair, cilia • Mucus membranes • Mucus and chemical secretions • Digestive enzymes in mouth • Stomach acid	• Inflammatory response • Complement proteins • Phagocytic cells • Natural killer (NK) cells	

There are two main parts to the vertebrate immune system. The innate immune system, which is made up of physical barriers and internal defenses, responds to all pathogens. The adaptive immune system is highly specific.

External and Chemical Barriers

The body has significant physical barriers to potential pathogens. The skin contains the protein keratin, which resists physical entry into cells. Other body surfaces, particularly those associated with body openings, are protected by the mucous membranes. The sticky mucus provides a physical trap for pathogens, preventing their movement deeper into the body. The openings of the body, such as the nose and ears, are protected by hairs that catch pathogens, and the mucous membranes of the upper respiratory tract have cilia that constantly move pathogens trapped in the mucus coat up to the mouth.

The skin and mucous membranes also create a chemical environment that is hostile to many microorganisms. The surface of the skin is acidic, which prevents bacterial growth. Saliva, mucus, and the tears of the eye contain an enzyme that breaks down bacterial cell walls. The stomach secretions create a highly acidic environment, which kills many pathogens entering the digestive system.

Finally, the surface of the body and the lower digestive system have a community of microorganisms such as bacteria, archaea, and fungi that coexist without harming the body. There is evidence that these organisms are highly beneficial to their host, combating disease-causing organisms and outcompeting them for nutritional resources provided by the host body. Despite these defenses, pathogens may enter the body through skin abrasions or punctures, or by collecting on mucosal surfaces in large numbers that overcome the protections of mucus or cilia.

Internal Defenses

When pathogens enter the body, the innate immune system responds with a variety of internal defenses. These include the inflammatory response, phagocytosis, natural killer cells, and the complement system. White blood cells in the blood and lymph recognize pathogens as foreign to the body. A **white blood cell** is larger than a red blood cell, is nucleated, and is typically able to move using amoeboid locomotion. Because they can move on their own, white blood cells can leave the blood to go to infected tissues. For

example, a **monocyte** is a type of white blood cell that circulates in the blood and lymph and develops into a macrophage after it moves into infected tissue. A **macrophage** is a large cell that engulfs foreign particles and pathogens. **Mast cells** are produced in the same way as white blood cells, but unlike circulating white blood cells, mast cells take up residence in connective tissues and especially mucosal tissues. They are responsible for releasing chemicals in response to physical injury. They also play a role in the allergic response, which will be discussed later in the chapter.

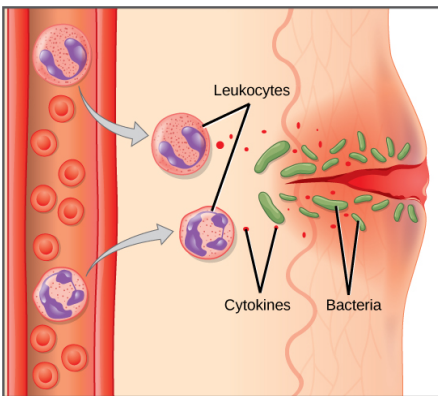
When a pathogen is recognized as foreign, chemicals called cytokines are released. A **cytokine** is a chemical messenger that regulates cell differentiation (form and function), proliferation (production), and gene expression to produce a variety of immune responses. Approximately 40 types of cytokines exist in humans. In addition to being released from white blood cells after pathogen recognition, cytokines are also released by the infected cells and bind to nearby uninfected cells, inducing those cells to release cytokines. This positive feedback loop results in a burst of cytokine production.

One class of early-acting cytokines is the interferons, which are released by infected cells as a warning to nearby uninfected cells. An **interferon** is a small protein that signals a viral infection to other cells. The interferons stimulate uninfected cells to produce compounds that interfere with viral replication. Interferons also activate macrophages and other cells.

The Inflammatory Response and Phagocytosis

The first cytokines to be produced encourage **inflammation**, a localized redness, swelling, heat, and pain. Inflammation is a response to physical trauma, such as a cut or a blow, chemical irritation, and infection by pathogens (viruses, bacteria, or fungi). The chemical signals that trigger an inflammatory response enter the extracellular fluid and cause capillaries to dilate (expand) and capillary walls to become more permeable, or leaky. The serum and other compounds leaking from capillaries cause swelling of the area, which in turn causes pain. Various kinds of white blood cells are attracted to the area of inflammation. The types of white blood cells that

arrive at an inflamed site depend on the nature of the injury or infecting pathogen. For example, a **neutrophil** is an early arriving white blood cell that engulfs and digests pathogens. Neutrophils are the most abundant white blood cells of the immune system ([\[link\]](#)). Macrophages follow neutrophils and take over the phagocytosis function and are involved in the resolution of an inflamed site, cleaning up cell debris and pathogens.



White blood cells (leukocytes) release chemicals to stimulate the inflammatory response following a cut in the skin.

Cytokines also send feedback to cells of the nervous system to bring about the overall symptoms of feeling sick, which include lethargy, muscle pain, and nausea. Cytokines also increase the core body temperature, causing a fever. The elevated temperatures of a fever inhibit the growth of pathogens and speed up cellular repair processes. For these reasons, suppression of fevers should be limited to those that are dangerously high.

Note:

Concept in Action



Check out this [23-second, stop-motion video](#) showing a neutrophil that searches and engulfs fungus spores during an elapsed time of 79 minutes.

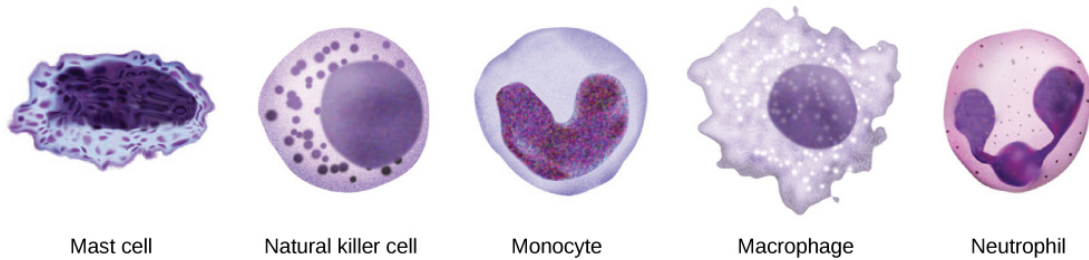
Natural Killer Cells

A **lymphocyte** is a white blood cell that contains a large nucleus ([link](#)). Most lymphocytes are associated with the adaptive immune response, but infected cells are identified and destroyed by natural killer cells, the only lymphocytes of the innate immune system. A **natural killer (NK) cell** is a lymphocyte that can kill cells infected with viruses (or cancerous cells). NK cells identify intracellular infections, especially from viruses, by the altered expression of **major histocompatibility class (MHC) I molecules** on the surface of infected cells. MHC class I molecules are proteins on the surfaces of all nucleated cells that provide a sample of the cell's internal environment at any given time. Unhealthy cells, whether infected or cancerous, display an altered MHC class I complement on their cell surfaces.



Lymphocytes, such as NK cells, are characterized by their large nuclei that actively absorb Wright stain and therefore appear dark colored under a microscope.
(credit: scale-bar data from Matt Russell)

After the NK cell detects an infected or tumor cell, it induces programmed cell death, or apoptosis. Phagocytic cells then come along and digest the cell debris left behind. NK cells are constantly patrolling the body and are an effective mechanism for controlling potential infections and preventing cancer progression. The various types of immune cells are shown in [\[link\]](#).



Cells involved in the innate immune response include mast cells, natural killer cells, and white blood cells, such as monocytes, macrophages and neutrophils.

Complement

An array of approximately 20 types of proteins, called a **complement system**, is also activated by infection or the activity of the cells of the adaptive immune system and functions to destroy extracellular pathogens. Liver cells and macrophages synthesize inactive forms of complement proteins continuously; these proteins are abundant in the blood serum and are capable of responding immediately to infecting microorganisms. The complement system is so named because it is complementary to the innate and adaptive immune system. Complement proteins bind to the surfaces of microorganisms and are particularly attracted to pathogens that are already tagged by the adaptive immune system. This “tagging” involves the attachment of specific proteins called antibodies (discussed in detail later) to the pathogen. When they attach, the antibodies change shape providing a binding site for one of the complement proteins. After the first few complement proteins bind, a cascade of binding in a specific sequence of proteins follows in which the pathogen rapidly becomes coated in complement proteins.

Complement proteins perform several functions, one of which is to serve as a marker to indicate the presence of a pathogen to phagocytic cells and enhance engulfment. Certain complement proteins can combine to open pores in microbial cell membranes and cause lysis of the cells.

Section Summary

The innate immune system consists first of physical and chemical barriers to infection including the skin and mucous membranes and their secretions, ciliated surfaces, and body hairs. The second line of defense is an internal defense system designed to counter pathogenic threats that bypass the physical and chemical barriers of the body. Using a combination of cellular and molecular responses, the innate immune system identifies the nature of a pathogen and responds with inflammation, phagocytosis, cytokine release, destruction by NK cells, or the complement system.

Review Questions

Exercise:

Problem:

Which of the following is a barrier against pathogens provided by the skin?

- a. low pH
- b. mucus
- c. tears
- d. cilia

Solution:

A

Exercise:

Problem:

Although interferons have several effects, they are particularly useful against infections with which type of pathogen?

- a. bacteria
- b. viruses

- c. fungi
 - d. helminths
-

Solution:

B

Exercise:

Problem:

Which innate immune system component uses MHC class I molecules directly in its defense strategy?

- a. macrophages
 - b. neutrophils
 - c. NK cells
 - d. interferon
-

Solution:

C

Free Response

Exercise:

Problem:

Different MHC class I molecules between donor and recipient cells can lead to rejection of a transplanted organ or tissue. Suggest a reason for this.

Solution:

If the MHC class I molecules expressed on donor cells differ from the MHC class I molecules expressed on recipient cells, NK cells may

identify the donor cells as not normal and produce enzymes to induce the donor cells to undergo apoptosis, which would destroy the transplanted organ.

Exercise:

Problem:

If a series of genetic mutations prevented some, but not all, of the complement proteins from binding antibodies or pathogens, would the entire complement system be compromised?

Solution:

The entire complement system would probably be affected even when only a few members were mutated such that they could no longer bind. Because the complement involves the binding of activated proteins in a specific sequence, when one or more proteins in the sequence is absent, the subsequent proteins would be incapable of binding to elicit the complement's pathogen-destructive effects.

Glossary

complement system

an array of approximately 20 soluble proteins of the innate immune system that enhance phagocytosis, bore holes in pathogens, and recruit lymphocytes

cytokine

a chemical messenger that regulates cell differentiation, proliferation, and gene expression to effect immune responses

inflammation

the localized redness, swelling, heat, and pain that results from the movement of leukocytes through opened capillaries to a site of infection

innate immunity

an immunity that occurs naturally because of genetic factors or physiology, and is not caused by infection or vaccination

interferon

a cytokine that inhibits viral replication

lymphocyte

a type of white blood cell that includes natural killer cells of the innate immune system and B and T cells of the adaptive immune system

macrophage

a large phagocytic cell that engulfs foreign particles and pathogens

major histocompatibility class (MHC) I

a group of proteins found on the surface of all nucleated cells that signals to immune cells whether the cell is normal or is infected or cancerous; it also provides the appropriate sites into which antigens can be loaded for recognition by lymphocytes

mast cell

a leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens

monocyte

a type of white blood cell that circulates in the blood and lymph and differentiates into a macrophage after it moves into infected tissue

natural killer (NK) cell

a lymphocyte that can kill cells infected with viruses or tumor cells

neutrophil

a phagocytic leukocyte that engulfs and digests pathogens

white blood cell

a nucleated cell found in the blood that is a part of the immune system; also called leukocytes

Adaptive Immunity

By the end of this section, you will be able to:

- Explain adaptive immunity
- Describe cell-mediated immune response and humoral immune response
- Describe immune tolerance

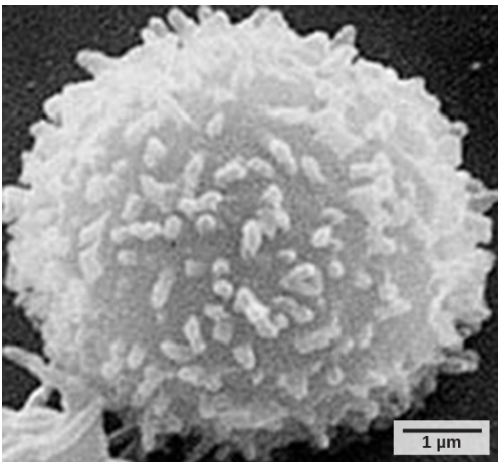
The adaptive, or acquired, immune response takes days or even weeks to become established—much longer than the innate response; however, adaptive immunity is more specific to an invading pathogen. **Adaptive immunity** is an immunity that occurs after exposure to an antigen either from a pathogen or a vaccination. An **antigen** is a molecule that stimulates a response in the immune system. This part of the immune system is activated when the innate immune response is insufficient to control an infection. In fact, without information from the innate immune system, the adaptive response could not be mobilized. There are two types of adaptive responses: the **cell-mediated immune response**, which is controlled by activated **T cells**, and the **humoral immune response**, which is controlled by activated **B cells** and antibodies. Activated T and B cells whose surface binding sites are specific to the molecules on the pathogen greatly increase in numbers and attack the invading pathogen. Their attack can kill pathogens directly or they can secrete antibodies that enhance the phagocytosis of pathogens and disrupt the infection. Adaptive immunity also involves a memory to give the host long-term protection from reinfection with the same type of pathogen; on reexposure, this host memory will facilitate a rapid and powerful response.

B and T Cells

Lymphocytes, which are white blood cells, are formed with other blood cells in the red bone marrow found in many flat bones, such as the shoulder or pelvic bones. The two types of lymphocytes of the adaptive immune response are B and T cells ([\[link\]](#)). Whether an immature lymphocyte becomes a B cell or T cell depends on where in the body it matures. The B cells remain in the bone marrow to mature (hence the name “B” for “bone

marrow”), while T cells migrate to the thymus, where they mature (hence the name “T” for “thymus”).

Maturation of a B or T cell involves becoming immunocompetent, meaning that it can recognize, by binding, a specific molecule or antigen (discussed below). During the maturation process, B and T cells that bind too strongly to the body’s own cells are eliminated in order to minimize an immune response against the body’s own tissues. Those cells that react weakly to the body’s own cells, but have highly specific receptors on their cell surfaces that allow them to recognize a foreign molecule, or antigen, remain. This process occurs during fetal development and continues throughout life. The specificity of this receptor is determined by the genetics of the individual and is present before a foreign molecule is introduced to the body or encountered. Thus, it is genetics and not experience that initially provides a vast array of cells, each capable of binding to a different specific foreign molecule. Once they are immunocompetent, the T and B cells will migrate to the spleen and lymph nodes where they will remain until they are called on during an infection. B cells are involved in the humoral immune response, which targets pathogens loose in blood and lymph, and T cells are involved in the cell-mediated immune response, which targets infected cells.

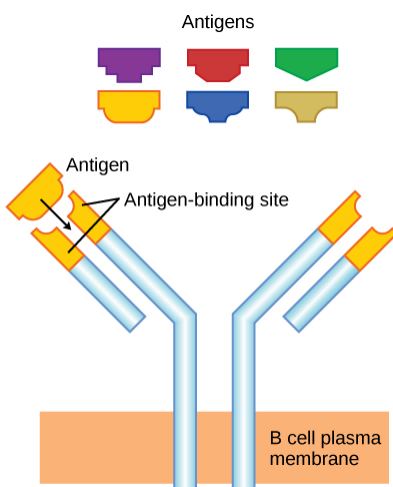


This scanning electron micrograph shows a T

lymphocyte. T and B cells are indistinguishable by light microscopy but can be differentiated experimentally by probing their surface receptors. (credit: modification of work by NCI; scale-bar data from Matt Russell)

Humoral Immune Response

As mentioned, an antigen is a molecule that stimulates a response in the immune system. Not every molecule is antigenic. B cells participate in a chemical response to antigens present in the body by producing specific antibodies that circulate throughout the body and bind with the antigen whenever it is encountered. This is known as the humoral immune response. As discussed, during maturation of B cells, a set of highly specific B cells are produced that have many antigen receptor molecules in their membrane ([link](#)).



B cell receptors are embedded in the membranes of B cells and bind a variety of antigens through their variable regions.

Each B cell has only one kind of antigen receptor, which makes every B cell different. Once the B cells mature in the bone marrow, they migrate to lymph nodes or other lymphatic organs. When a B cell encounters the antigen that binds to its receptor, the antigen molecule is brought into the cell by endocytosis and reappears on the surface of the cell bound to an **MHC class II molecule**. When this process is complete, the B cell is sensitized. In most cases, the sensitized B cell must then encounter a specific kind of T cell, called a helper T cell, before it is activated. The helper T cell must already have been activated through an encounter with the antigen (discussed below).

The helper T cell binds to the antigen-MHC class II complex and is induced to release cytokines that induce the B cell to divide rapidly, which makes thousands of identical (clonal) cells. These daughter cells become either plasma cells or memory B cells. The memory B cells remain inactive at this point, until another later encounter with the antigen, caused by a reinfection by the same bacteria or virus, results in them dividing into a new population of plasma cells. The plasma cells, on the other hand, produce and secrete large quantities, up to 100 million molecules per hour, of antibody molecules. An **antibody**, also known as an immunoglobulin (Ig), is a protein that is produced by plasma cells after stimulation by an antigen. Antibodies are the agents of humoral immunity. Antibodies occur in the blood, in gastric and mucus secretions, and in breast milk. Antibodies in these bodily fluids can bind pathogens and mark them for destruction by phagocytes before they can infect cells.

These antibodies circulate in the blood stream and lymphatic system and bind with the antigen whenever it is encountered. The binding can fight infection in several ways. Antibodies can bind to viruses or bacteria and interfere with the chemical interactions required for them to infect or bind to other cells. The antibodies may create bridges between different particles containing antigenic sites clumping them all together and preventing their proper functioning. The antigen-antibody complex stimulates the complement system described previously, destroying the cell bearing the antigen. Phagocytic cells, such as those already described, are attracted by the antigen-antibody complexes, and phagocytosis is enhanced when the complexes are present. Finally, antibodies stimulate inflammation, and their presence in mucus and on the skin prevents pathogen attack.

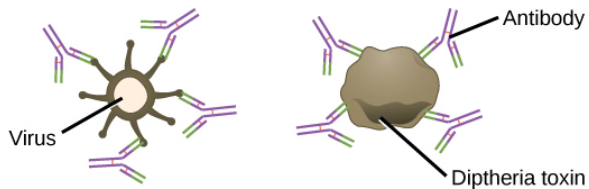
Antibodies coat extracellular pathogens and neutralize them by blocking key sites on the pathogen that enhance their infectivity (such as receptors that “dock” pathogens on host cells) ([link](#)). Antibody neutralization can prevent pathogens from entering and infecting host cells. The neutralized antibody-coated pathogens can then be filtered by the spleen and eliminated in urine or feces.

Antibodies also mark pathogens for destruction by phagocytic cells, such as macrophages or neutrophils, in a process called opsonization. In a process called complement fixation, some antibodies provide a place for complement proteins to bind. The combination of antibodies and complement promotes rapid clearing of pathogens.

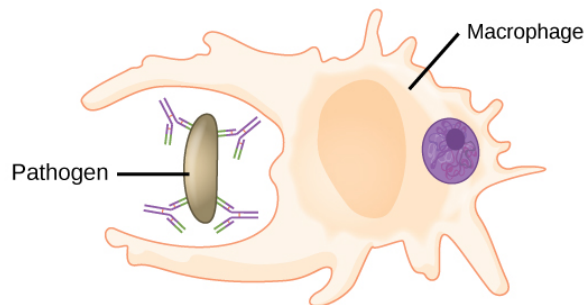
The production of antibodies by plasma cells in response to an antigen is called **active immunity** and describes the host’s active response of the immune system to an infection or to a vaccination. There is also a **passive immune** response where antibodies come from an outside source, instead of the individual’s own plasma cells, and are introduced into the host. For example, antibodies circulating in a pregnant woman’s body move across the placenta into the developing fetus. The child benefits from the presence of these antibodies for up to several months after birth. In addition, a passive immune response is possible by injecting antibodies into an individual in the form of an antivenom to a snake-bite toxin or antibodies in blood serum to help fight a hepatitis infection. This gives immediate

protection since the body does not need the time required to mount its own response.

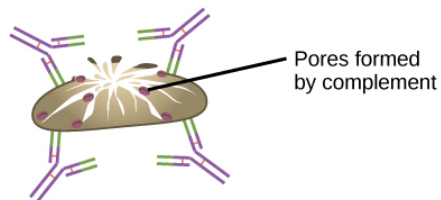
(a) Neutralization Antibodies prevent a virus or toxic protein from binding their target.



(b) Opsonization A pathogen tagged by antibodies is consumed by a macrophage or neutrophil.



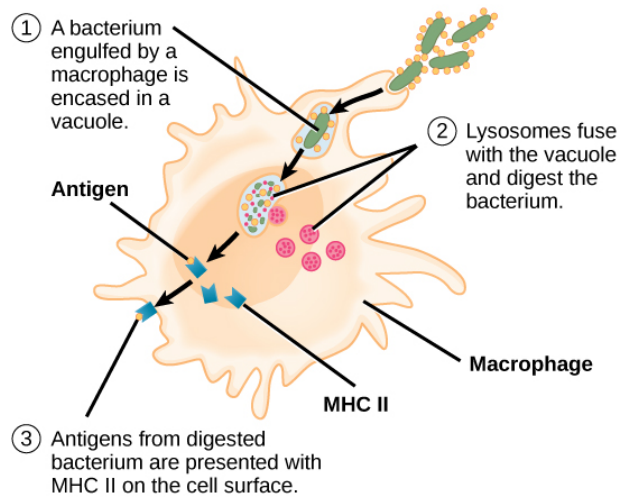
(c) Complement activation Antibodies attached to the surface of a pathogen cell activate the complement system.



Antibodies may inhibit infection by (a) preventing the antigen from binding its target, (b) tagging a pathogen for destruction by macrophages or neutrophils, or (c) activating the complement cascade.

Cell-Mediated Immunity

Unlike B cells, T lymphocytes are unable to recognize pathogens without assistance. Instead, dendritic cells and macrophages first engulf and digest pathogens into hundreds or thousands of antigens. Then, an **antigen-presenting cell (APC)** detects, engulfs, and informs the adaptive immune response about an infection. When a pathogen is detected, these APCs will engulf and break it down through phagocytosis. Antigen fragments will then be transported to the surface of the APC, where they will serve as an indicator to other immune cells. A **dendritic cell** is an immune cell that mops up antigenic materials in its surroundings and presents them on its surface. Dendritic cells are located in the skin, the linings of the nose, lungs, stomach, and intestines. These positions are ideal locations to encounter invading pathogens. Once they are activated by pathogens and mature to become APCs they migrate to the spleen or a lymph node. Macrophages also function as APCs. After phagocytosis by a macrophage, the phagocytic vesicle fuses with an intracellular lysosome. Within the resulting phagolysosome, the components are broken down into fragments; the fragments are then loaded onto MHC class II molecules and are transported to the cell surface for antigen presentation ([\[link\]](#)). Helper T cells cannot properly respond to an antigen unless it is processed and embedded in an MHC class II molecule. The APCs express MHC class II on their surfaces, and when combined with a foreign antigen, these complexes signal an invader.



An antigen-presenting cell (APC), such as a macrophage, engulfs a foreign antigen, partially digests it in a lysosome, and then embeds it in an MHC class II molecule for presentation at the cell surface. Lymphocytes of the adaptive immune response must interact with antigen-embedded MHC class II molecules to mature into functional immune cells.

Note:
Concept in Action



View this [animation from Rockefeller University](#) to see how dendritic cells act as sentinels in the body's immune system.

T cells have many functions. Some respond to APCs of the innate immune system and indirectly induce immune responses by releasing cytokines. Others stimulate B cells to start the humoral response as described previously. Another type of T cell detects APC signals and directly kills the infected cells, while some are involved in suppressing inappropriate immune reactions to harmless or “self” antigens.

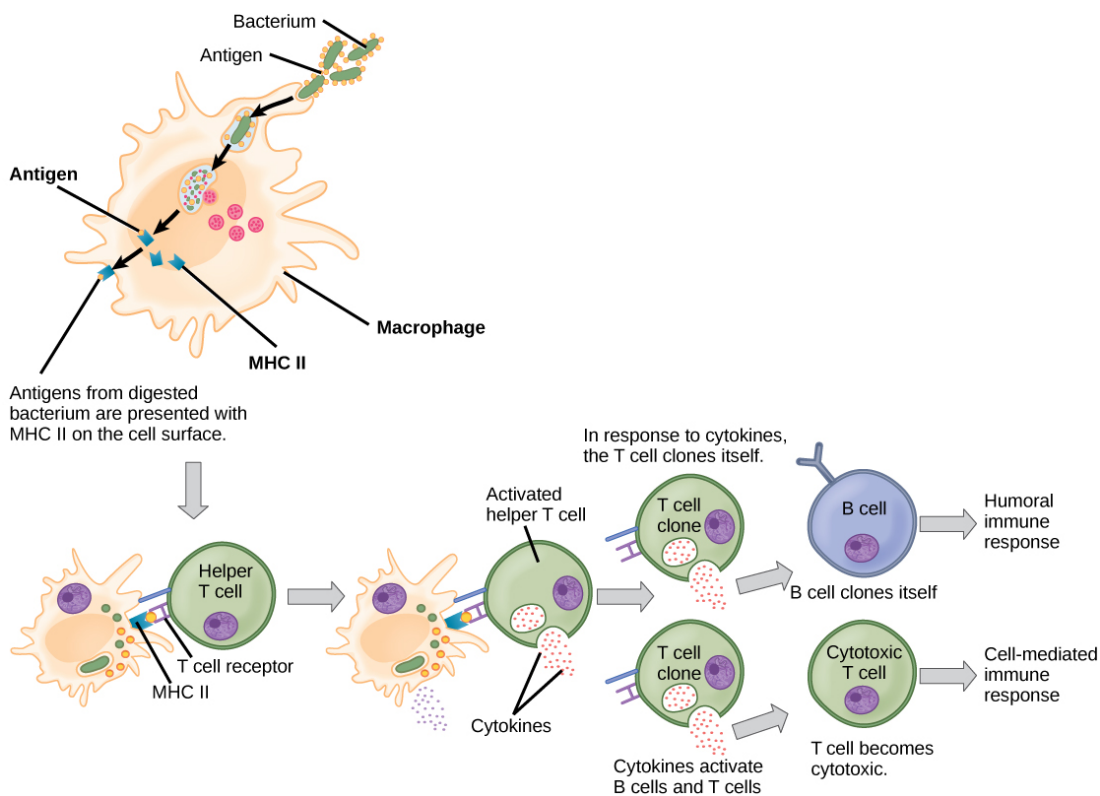
There are two main types of T cells: helper T lymphocytes (T_H) and the cytotoxic T lymphocytes (T_C). The T_H lymphocytes function indirectly to tell other immune cells about potential pathogens. T_H lymphocytes recognize specific antigens presented by the MHC class II complexes of APCs. There are two populations of T_H cells: T_H1 and T_H2 . T_H1 cells secrete cytokines to enhance the activities of macrophages and other T cells. T_H2 cells stimulate naïve B cells to secrete antibodies. Whether a T_H1 or a T_H2 immune response develops depends on the specific types of cytokines secreted by cells of the innate immune system, which in turn depends on the nature of the invading pathogen.

Cytotoxic T cells (T_C) are the key component of the cell-mediated part of the adaptive immune system and attack and destroy infected cells. T_C cells are particularly important in protecting against viral infections; this is because viruses replicate within cells where they are shielded from extracellular contact with circulating antibodies. Once activated, the T_C creates a large clone of cells with one specific set of cell-surface receptors, as in the case with proliferation of activated B cells. As with B cells, the clone includes active T_C cells and inactive memory T_C cells. The resulting active T_C cells then identify infected host cells. Because of the time required to generate a population of clonal T and B cells, there is a delay in the adaptive immune response compared to the innate immune response.

T_C cells attempt to identify and destroy infected cells before the pathogen can replicate and escape, thereby halting the progression of intracellular infections. T_C cells also support NK lymphocytes to destroy early cancers.

Cytokines secreted by the T_H1 response that stimulates macrophages also stimulate T_C cells and enhance their ability to identify and destroy infected cells and tumors. A summary of how the humoral and cell-mediated immune responses are activated appears in [\[link\]](#).

B plasma cells and T_C cells are collectively called **effector cells** because they are involved in “effecting” (bringing about) the immune response of killing pathogens and infected host cells.



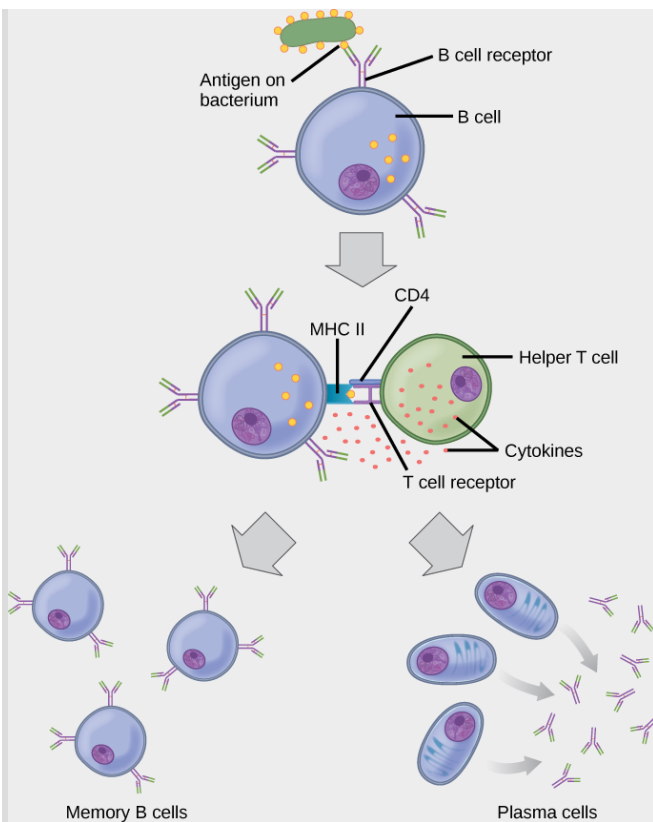
A helper T cell becomes activated by binding to an antigen presented by an APC via the MHCII receptor, causing it to release cytokines. Depending on the cytokines released, this activates either the humoral or the cell-mediated immune response.

Immunological Memory

The adaptive immune system has a memory component that allows for a rapid and large response upon reinvasion of the same pathogen. During the adaptive immune response to a pathogen that has not been encountered before, known as the **primary immune response**, plasma cells secreting antibodies and differentiated T cells increase, then plateau over time. As B and T cells mature into effector cells, a subset of the naïve populations differentiates into B and T memory cells with the same antigen specificities ([\[link\]](#)). A **memory cell** is an antigen-specific B or T lymphocyte that does not differentiate into an effector cell during the primary immune response, but that can immediately become an effector cell on reexposure to the same pathogen. As the infection is cleared and pathogenic stimuli subside, the effectors are no longer needed and they undergo apoptosis. In contrast, the memory cells persist in the circulation.

Note:

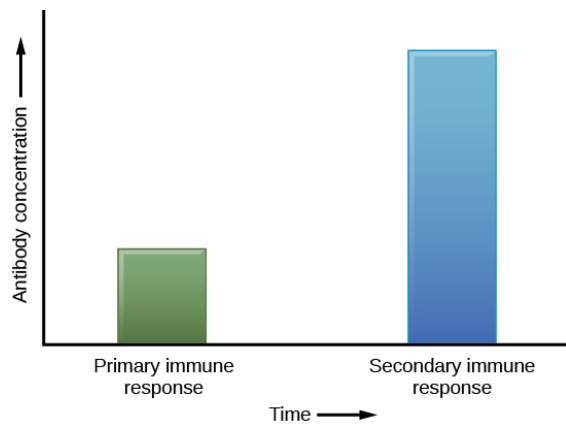
Art Connection



After initially binding an antigen to the B cell receptor, a B cell internalizes the antigen and presents it on MHC class II. A helper T cell recognizes the MHC class II- antigen complex and activates the B cell. As a result, memory B cells and plasma cells are made.

The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

If the pathogen is never encountered again during the individual's lifetime, B and T memory cells will circulate for a few years or even several decades and will gradually die off, having never functioned as effector cells. However, if the host is re-exposed to the same pathogen type, circulating memory cells will immediately differentiate into plasma cells and T_C cells without input from APCs or T_H cells. This is known as the **secondary immune response**. One reason why the adaptive immune response is delayed is because it takes time for naïve B and T cells with the appropriate antigen specificities to be identified, activated, and proliferate. On reinfection, this step is skipped, and the result is a more rapid production of immune defenses. Memory B cells that differentiate into plasma cells output tens to hundreds-fold greater antibody amounts than were secreted during the primary response ([\[link\]](#)). This rapid and dramatic antibody response may stop the infection before it can even become established, and the individual may not realize they had been exposed.



In the primary response to infection, antibodies are secreted first from plasma cells. Upon re-exposure to the same pathogen, memory cells differentiate into antibody-secreting plasma cells that output a greater

amount of antibody for a longer period of time.

Vaccination is based on the knowledge that exposure to noninfectious antigens, derived from known pathogens, generates a mild primary immune response. The immune response to vaccination may not be perceived by the host as illness but still confers immune memory. When exposed to the corresponding pathogen to which an individual was vaccinated, the reaction is similar to a secondary exposure. Because each reinfection generates more memory cells and increased resistance to the pathogen, some vaccine courses involve one or more booster vaccinations to mimic repeat exposures.

The Lymphatic System

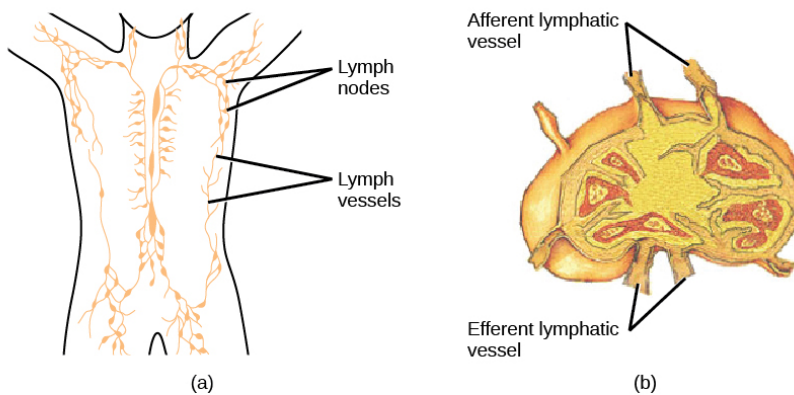
Lymph is the watery fluid that bathes tissues and organs and contains protective white blood cells but does not contain erythrocytes. Lymph moves about the body through the lymphatic system, which is made up of vessels, lymph ducts, lymph glands, and organs, such as tonsils, adenoids, thymus, and spleen.

Although the immune system is characterized by circulating cells throughout the body, the regulation, maturation, and intercommunication of immune factors occur at specific sites. The blood circulates immune cells, proteins, and other factors through the body. Approximately 0.1 percent of all cells in the blood are leukocytes, which include monocytes (the precursor of macrophages) and lymphocytes. Most cells in the blood are red blood cells. Cells of the immune system can travel between the distinct lymphatic and blood circulatory systems, which are separated by interstitial space, by a process called extravasation (passing through to surrounding tissue).

Recall that cells of the immune system originate from stem cells in the bone marrow. B cell maturation occurs in the bone marrow, whereas progenitor

cells migrate from the bone marrow and develop and mature into naïve T cells in the organ called the thymus.

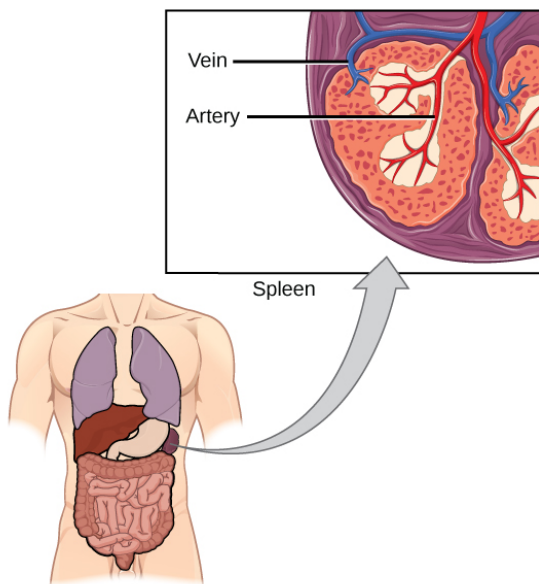
On maturation, T and B lymphocytes circulate to various destinations. Lymph nodes scattered throughout the body house large populations of T and B cells, dendritic cells, and macrophages ([\[link\]](#)). Lymph gathers antigens as it drains from tissues. These antigens then are filtered through lymph nodes before the lymph is returned to circulation. APCs in the lymph nodes capture and process antigens and inform nearby lymphocytes about potential pathogens.



(a) Lymphatic vessels carry a clear fluid called lymph throughout the body. The liquid passes through (b) lymph nodes that filter the lymph that enters the node through afferent vessels and leaves through efferent vessels; lymph nodes are filled with lymphocytes that purge infecting cells. (credit a: modification of work by NIH; credit b: modification of work by NCI, NIH)

The spleen houses B and T cells, macrophages, dendritic cells, and NK cells ([\[link\]](#)). The spleen is the site where APCs that have trapped foreign particles in the blood can communicate with lymphocytes. Antibodies are

synthesized and secreted by activated plasma cells in the spleen, and the spleen filters foreign substances and antibody-complexed pathogens from the blood. Functionally, the spleen is to the blood as lymph nodes are to the lymph.



The spleen functions to immunologically filter the blood and allow for communication between cells corresponding to the innate and adaptive immune responses. (credit: modification of work by NCI, NIH)

Mucosal Immune System

The innate and adaptive immune responses compose the systemic immune system (affecting the whole body), which is distinct from the mucosal

immune system. Mucosa associated lymphoid tissue (MALT) is a crucial component of a functional immune system because mucosal surfaces, such as the nasal passages, are the first tissues onto which inhaled or ingested pathogens are deposited. The mucosal tissue includes the mouth, pharynx, and esophagus, and the gastrointestinal, respiratory, and urogenital tracts.

Mucosal immunity is formed by MALT, which functions independently of the systemic immune system, and which has its own innate and adaptive components. MALT is a collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body. This tissue functions as the immune barrier and response in areas of the body with direct contact to the external environment. The systemic and mucosal immune systems use many of the same cell types. Foreign particles that make their way to MALT are taken up by absorptive epithelial cells and delivered to APCs located directly below the mucosal tissue. APCs of the mucosal immune system are primarily dendritic cells, with B cells and macrophages having minor roles. Processed antigens displayed on APCs are detected by T cells in the MALT and at the tonsils, adenoids, appendix, or the mesenteric lymph nodes of the intestine. Activated T cells then migrate through the lymphatic system and into the circulatory system to mucosal sites of infection.

Immune Tolerance

The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances, and more importantly, so that it does not attack “self.” The acquired ability to prevent an unnecessary or harmful immune response to a detected foreign substance known not to cause disease, or self-antigens, is described as **immune tolerance**. The primary mechanism for developing immune tolerance to self-antigens occurs during the selection for weakly self-binding cells during T and B lymphocyte maturation. There are populations of T cells that suppress the immune response to self-antigens and that suppress the immune response after the infection has cleared to minimize host cell damage induced by inflammation and cell lysis. Immune tolerance is especially well developed in the mucosa of the upper digestive system because of the tremendous number of foreign substances (such as food proteins) that APCs of the oral

cavity, pharynx, and gastrointestinal mucosa encounter. Immune tolerance is brought about by specialized APCs in the liver, lymph nodes, small intestine, and lung that present harmless antigens to a diverse population of regulatory T (T_{reg}) cells, specialized lymphocytes that suppress local inflammation and inhibit the secretion of stimulatory immune factors. The combined result of T_{reg} cells is to prevent immunologic activation and inflammation in undesired tissue compartments and to allow the immune system to focus on pathogens instead.

Section Summary

The adaptive immune response is a slower-acting, longer-lasting, and more specific response than the innate response. However, the adaptive response requires information from the innate immune system to function. APCs display antigens on MHC molecules to naïve T cells. T cells with cell-surface receptors that bind a specific antigen will bind to that APC. In response, the T cells differentiate and proliferate, becoming T_{H} cells or T_{C} cells. T_{H} cells stimulate B cells that have engulfed and presented pathogen-derived antigens. B cells differentiate into plasma cells that secrete antibodies, whereas T_{C} cells destroy infected or cancerous cells. Memory cells are produced by activated and proliferating B and T cells and persist after a primary exposure to a pathogen. If re-exposure occurs, memory cells differentiate into effector cells without input from the innate immune system. The mucosal immune system is largely independent of the systemic immune system but functions in parallel to protect the extensive mucosal surfaces of the body. Immune tolerance is brought about by T_{reg} cells to limit reactions to harmless antigens and the body's own molecules.

Art Connections

Exercise:

Problem:

[\[link\]](#) The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

Solution:

[\[link\]](#) If the blood of the mother and fetus mixes, memory cells that recognize the Rh antigen of the fetus can form in the mother late in the first pregnancy. During subsequent pregnancies, these memory cells launch an immune attack on the fetal blood cells of an Rh-positive fetus. Injection of anti-Rh antibody during the first pregnancy prevents the immune response from occurring.

Review Questions**Exercise:**

Problem: The humoral immune response depends on which cells?

- a. T_C cells
 - b. B cells
 - c. B and T_H cells
 - d. T_C and T_H cells
-

Solution:

C

Exercise:

Problem:

The fact that the body does not normally mount an immune response to the molecules in food is an example of _____.

- a. secondary immune response
- b. immunological memory
- c. immune tolerance
- d. passive immunity

Solution:

C

Exercise:**Problem:**

Foreign particles circulating in the blood are filtered by the _____.

- a. spleen
- b. lymph nodes
- c. MALT
- d. lymph

Solution:

A

Free Response**Exercise:****Problem:**

How do B and T cells differ with respect to antigens that they bind?

Solution:

T cells bind antigens that have been digested and embedded in MHC molecules by APCs. In contrast, B cells function as APCs to bind intact, unprocessed antigens.

Exercise:**Problem:**

Why is the immune response after reinfection much faster than the adaptive immune response after the initial infection?

Solution:

Upon reinfection, the memory cells will immediately differentiate into plasma cells and CTLs without input from APCs or T_H cells. In contrast, the adaptive immune response to the initial infection requires time for naïve B and T cells with the appropriate antigen specificities to be identified and activated.

Glossary

active immunity

an immunity that occurs as a result of the activity of the body's own cells rather than from antibodies acquired from an external source

adaptive immunity

a specific immune response that occurs after exposure to an antigen either from a pathogen or a vaccination

antibody

a protein that is produced by plasma cells after stimulation by an antigen; also known as an immunoglobulin

antigen

a macromolecule that reacts with cells of the immune system and which may or may not have a stimulatory effect

antigen-presenting cell (APC)

an immune cell that detects, engulfs, and informs the adaptive immune response about an infection by presenting the processed antigen on its cell surface

B cell

a lymphocyte that matures in the bone marrow

cell-mediated immune response

an adaptive immune response that is controlled by T cells

cytotoxic T lymphocyte (T_C)

an adaptive immune cell that directly kills infected cells via enzymes, and that releases cytokines to enhance the immune response

dendritic cell

an immune cell that processes antigen material and presents it on the surface of its cell in MHC class II molecules and induces an immune response in other cells

effector cell

a lymphocyte that has differentiated, such as a B cell, plasma cell, or cytotoxic T cell

helper T lymphocyte (T_H)

a cell of the adaptive immune system that binds APCs via MHC class II molecules and stimulates B cells or secretes cytokines to initiate the immune response

humoral immune response

the adaptive immune response that is controlled by activated B cells and antibodies

immune tolerance

an acquired ability to prevent an unnecessary or harmful immune response to a detected foreign body known not to cause disease

lymph

the watery fluid present in the lymphatic circulatory system that bathes tissues and organs with protective white blood cells and does not contain erythrocytes

memory cell

an antigen-specific B or T lymphocyte that does not differentiate into an effector cell during the primary immune response but that can immediately become an effector cell on reexposure to the same pathogen

major histocompatibility class (MHC) II molecule

a protein found on the surface of antigen-presenting cells that signals to immune cells whether the cell is normal or is infected or cancerous; it provides the appropriate template into which antigens can be loaded for recognition by lymphocytes

passive immunity

an immunity that does not result from the activity of the body's own immune cells but by transfer of antibodies from one individual to another

primary immune response

the response of the adaptive immune system to the first exposure to an antigen

secondary immune response

the response of the adaptive immune system to a second or later exposure to an antigen mediated by memory cells

T cell

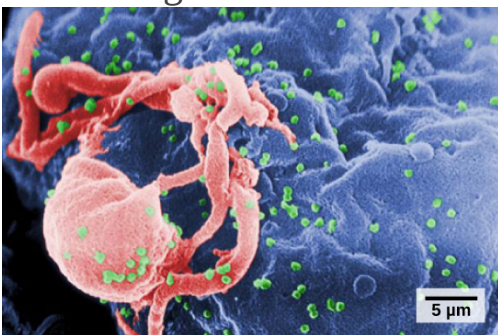
a lymphocyte that matures in the thymus gland

Disruptions in the Immune System

By the end of this section, you will be able to:

- Describe hypersensitivity
- Define autoimmunity

A functioning immune system is essential for survival, but even the sophisticated cellular and molecular defenses of the mammalian immune response can be defeated by pathogens at virtually every step. In the competition between immune protection and pathogen evasion, pathogens have the advantage of more rapid evolution because of their shorter generation time, large population sizes and often higher mutation rates. Thus pathogens have evolved a diverse array of immune escape mechanisms. For instance, *Streptococcus pneumoniae* (the bacterium that causes pneumonia and meningitis) surrounds itself with a capsule that inhibits phagocytes from engulfing it and displaying antigens to the adaptive immune system. *Staphylococcus aureus* (the bacterium that can cause skin infections, abscesses, and meningitis) synthesizes a toxin called leukocidin that kills phagocytes after they engulf the bacterium. Other pathogens can also hinder the adaptive immune system. HIV infects T_H cells using their CD4 surface molecules, gradually depleting the number of T_H cells in the body ([link](#)); this inhibits the adaptive immune system's capacity to generate sufficient responses to infection or tumors. As a result, HIV-infected individuals often suffer from infections that would not cause illness in people with healthy immune systems but which can cause devastating illness to immune-compromised individuals.



HIV (green) is shown
budding from a
lymphocyte cell (red) in

culture. (credit:
modification of work by
C. Goldsmith, CDC;
scale-bar data from Matt
Russell)

Inappropriate responses of immune cells and molecules themselves can also disrupt the proper functioning of the entire system, leading to host-cell damage that can become fatal.

Immunodeficiency

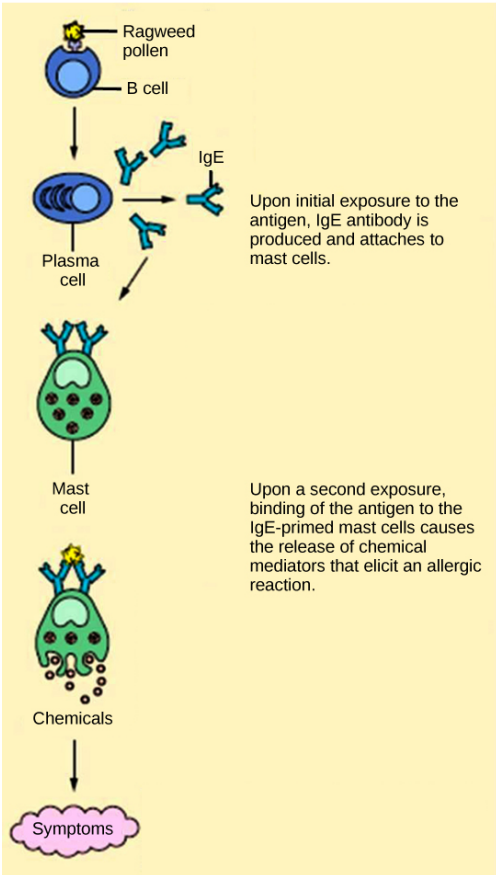
Immunodeficiency is a failure, insufficiency, or delay in the response of the immune system, which may be acquired or inherited. Immunodeficiency can allow pathogens or tumor cells to gain a foothold and replicate or proliferate to high enough levels so that the immune system becomes overwhelmed. Immunodeficiency can be acquired as a result of infection with certain pathogens that attack the cells of the immune system itself (such as HIV), chemical exposure (including certain medical treatments such as chemotherapy), malnutrition, or extreme stress. For instance, radiation exposure can destroy populations of lymphocytes and elevate an individual's susceptibility to infections and cancer. Rarely, primary immunodeficiencies that are present from birth may also occur. For example, severe combined immunodeficiency disease (SCID) is a condition in which children are born without functioning B or T cells.

Hypersensitivities

A maladaptive immune response toward harmless foreign substances or self-antigens that occur after tissue sensitization is termed a **hypersensitivity**. Types of hypersensitivities include immediate, delayed, and autoimmune. A large proportion of the human population is affected by one or more types of hypersensitivity.

Allergies

The immune reaction that results from immediate hypersensitivities in which an antibody-mediated immune response occurs within minutes of exposure to a usually harmless antigen is called an **allergy**. In the United States, 20 percent of the population exhibits symptoms of allergy or asthma, whereas 55 percent test positive against one or more allergens. On initial exposure to a potential allergen, an allergic individual synthesizes antibodies through the typical process of APCs presenting processed antigen to T_H cells that stimulate B cells to produce the antibodies. The antibody molecules interact with mast cells embedded in connective tissues. This process primes, or sensitizes, the tissue. On subsequent exposure to the same allergen, antibody molecules on mast cells bind the antigen and stimulate the mast cell to release histamine and other inflammatory chemicals; these chemical mediators then recruit eosinophils (a type of white blood cell), which also appear to be adapted to responding to parasitic worms ([\[link\]](#)). Eosinophils release factors that enhance the inflammatory response and the secretions of mast cells. The effects of an allergic reaction range from mild symptoms like sneezing and itchy, watery eyes to more severe or even life-threatening reactions involving intensely itchy welts or hives, airway constriction with severe respiratory distress, and plummeting blood pressure caused by dilating blood vessels and fluid loss from the circulatory system. This extreme reaction, typically in response to an allergen introduced to the circulatory system, is known as anaphylactic shock. Antihistamines are an insufficient counter to anaphylactic shock and if not treated with epinephrine to counter the blood pressure and breathing effects, this condition can be fatal.



On first exposure to an allergen, an antibody is synthesized by plasma cells in response to a harmless antigen. The antibodies bind to mast cells, and on secondary exposure, the mast cells release histamines and other modulators that cause the symptoms of allergy. (credit: modification of work by NIH)

Delayed hypersensitivity is a cell-mediated immune response that takes approximately one to two days after secondary exposure for a maximal reaction. This type of hypersensitivity involves the T_H1 cytokine-mediated inflammatory response and may cause local tissue lesions or contact dermatitis (rash or skin irritation). Delayed hypersensitivity occurs in some individuals in response to contact with certain types of jewelry or cosmetics. Delayed hypersensitivity facilitates the immune response to poison ivy and is also the reason why the skin test for tuberculosis results in a small region of inflammation on individuals who were previously exposed to *Mycobacterium tuberculosis*, the organism that causes tuberculosis.

Note:

Concept in Action

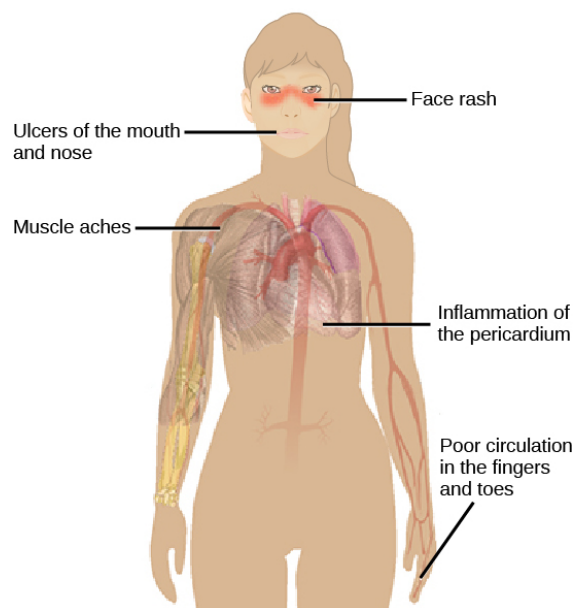


Try your hand at diagnosing an allergic reaction by selecting one of the [interactive case studies](#) at the World Allergy Organization website.

Autoimmunity

Autoimmunity is a type of hypersensitivity to self-antigens that affects approximately five percent of the population. Most types of autoimmunity involve the humoral immune response. An antibody that inappropriately marks self-components as foreign is termed an **autoantibody**. In patients with myasthenia gravis, an autoimmune disease, muscle-cell receptors that induce contraction in response to acetylcholine are targeted by antibodies. The result is muscle weakness that may include marked difficulty with fine or gross motor functions. In systemic lupus erythematosus, a diffuse autoantibody response to the individual's own DNA and proteins results in

various systemic diseases ([\[link\]](#)). Systemic lupus erythematosus may affect the heart, joints, lungs, skin, kidneys, central nervous system, or other tissues, causing tissue damage through antibody binding, complement recruitment, lysis, and inflammation.



Systemic lupus erythematosus is characterized by autoimmunity to the individual's own DNA and/or proteins, which leads to varied dysfunction of the organs. (credit: modification of work by Mikael Häggström)

Autoimmunity can develop with time and its causes may be rooted in molecular mimicry, a situation in which one molecule is similar enough in shape to another molecule that it binds the same immune receptors.

Antibodies and T-cell receptors may bind self-antigens that are structurally similar to pathogen antigens. As an example, infection with *Streptococcus pyogenes* (the bacterium that causes strep throat) may generate antibodies or T cells that react with heart muscle, which has a similar structure to the surface of *S. pyogenes*. These antibodies can damage heart muscle with autoimmune attacks, leading to rheumatic fever. Insulin-dependent (Type 1) diabetes mellitus arises from a destructive inflammatory T_H1 response against insulin-producing cells of the pancreas. Patients with this autoimmunity must be treated with regular insulin injections.

Section Summary

Immune disruptions may involve insufficient immune responses or inappropriate immune responses. Immunodeficiency increases an individual's susceptibility to infections and cancers. Hypersensitivities are misdirected responses either to harmless foreign particles, as in the case of allergies, or to the individual's own tissues, as in the case of autoimmunity. Reactions to self-components may be the result of molecular mimicry.

Review Questions

Exercise:

Problem: Allergy to pollen is classified as _____.

- a. an autoimmune reaction
- b. immunodeficiency
- c. delayed hypersensitivity
- d. immediate hypersensitivity

Solution:

D

Exercise:

Problem: A potential cause of acquired autoimmunity is _____.

- a. tissue hypersensitivity
- b. molecular mimicry
- c. histamine release
- d. radiation exposure

Solution:

B

Exercise:

Problem: Autoantibodies are probably involved in _____.

- a. reactions to poison ivy
- b. pollen allergies
- c. systemic lupus erythematosus
- d. HIV/AIDS

Solution:

C

Free Response

Exercise:

Problem:

Some photographers develop a sensitivity to certain film developing chemicals leading to severe rashes on their hands such that they are unable to work with them. Explain what is probably happening.

Solution:

This is probably a delayed sensitivity reaction to one or more chemicals in the developer. An initial exposure would have sensitized the individual to the chemical and then subsequent exposures will induce a delayed inflammation reaction a day or two after exposure.

Glossary

allergy

an immune reaction that results from immediate hypersensitivities in which an antibody-mediated immune response occurs within minutes of exposure to a harmless antigen

autoantibody

an antibody that incorrectly marks “self” components as foreign and stimulates the immune response

autoimmunity

a type of hypersensitivity to self-antigens

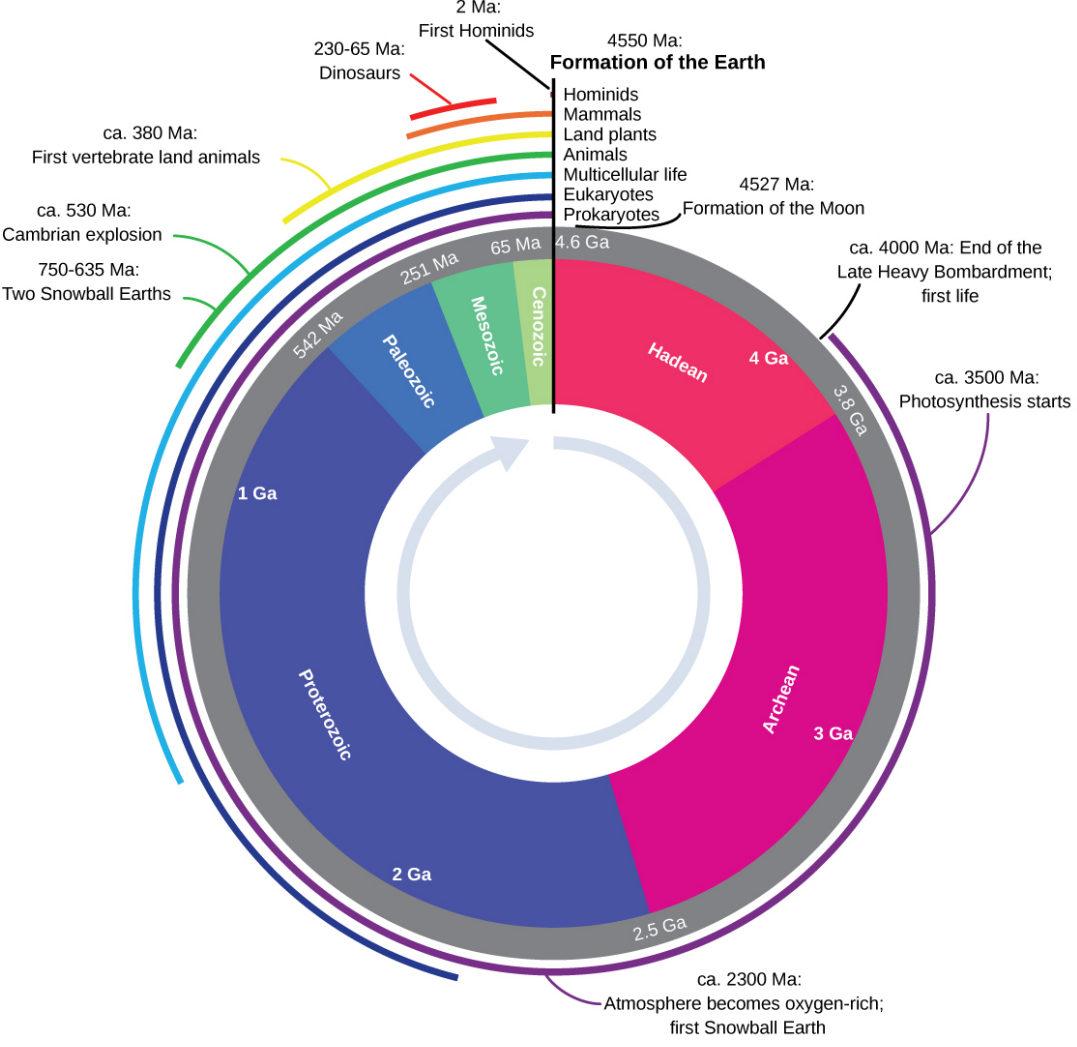
hypersensitivity

a spectrum of inappropriate immune responses toward harmless foreign particles or self-antigens; occurs after tissue sensitization and includes immediate-type (allergy), delayed-type, and autoimmunity

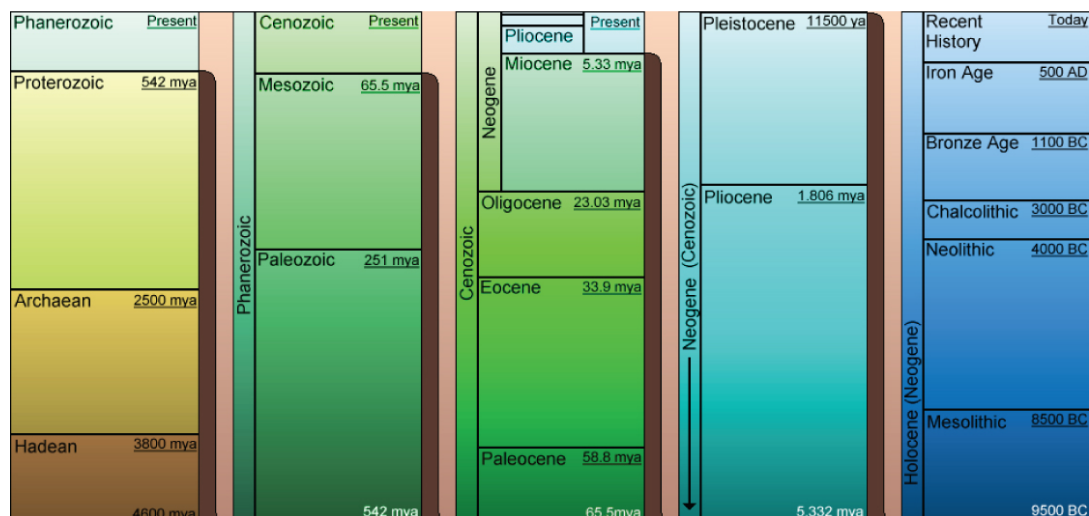
immunodeficiency

a failure, insufficiency, or delay at any level of the immune system, which may be acquired or inherited

Geological Time



Geological Time Clock



Geological Time Chart
(credit: Richard S. Murphy, Jr.)

Measurements and the Metric System

Measurements and the Metric System

Measurements and the Metric System				
Measurement	Unit	Abbreviation	Metric Equivalent	Approximate Standard Equivalent
Length	nanometer	nm	1 nm = 10^{-9} m	1 mm = 0.039 inch 1 cm = 0.394 inch 1 m = 39.37 inches 1 m = 3.28 feet 1 m = 1.093 yards 1 km = 0.621 miles
	micrometer	µm	1 µm = 10^{-6} m	
	millimeter	mm	1 mm = 0.001 m	
	centimeter	cm	1 cm = 0.01 m	
	meter	m	1 m = 100 cm 1 m = 1000 mm	
	kilometer	km	1 km = 1000 m	
Mass	microgram	µg	1 µg = 10^{-6} g	1 g = 0.035 ounce 1 kg = 2.205
	milligram	mg	1 mg = 10^{-3} g	

Measurements and the Metric System				pounds
Measurement	Unit	Abbreviation	Metric Equivalent	Approximate Standard Equivalent
	gram	g	1 g = 1000 mg	1 ml = 0.034 fluid ounce 1 l = 1.057 quarts 1 kl = 264.172 gallons
	kilogram	kg	1 kg = 1000 g	
Volume	microliter	μl	1 μl = 10 ⁻⁶ l	
	milliliter	ml	1 ml = 10 ⁻³ l	
	liter	l	1 l = 1000 ml	
	kiloliter	kl	1 kl = 1000 l	
Area	square centimeter	cm ²	1 cm ² = 100 mm ²	1 cm ² = 0.155 square inch 1 m ² = 10.764 square feet 1 m ² = 1.196 square yards 1 ha = 2.471 acres
	square meter	m ²	1 m ² = 10,000 cm ²	
	hectare	ha	1 ha = 10,000 m ²	
Temperature	Celsius	°C	—	1 °C = 5/9 × (°F – 32)

